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Proceedings— Symposium on Shrub Ecophysiology and Biotechnology





SHRUB RESEARCH CONSORTIUM

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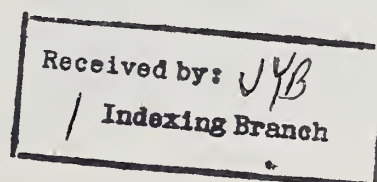
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INTRODUCTION: SHRUB ECOPHYSIOLOGY AND BIOTECHNOLOGY

E. Durant McArthur, Arthur Wallace, and Marshall R. Haferkamp

This is the fifth in a series of symposium proceedings on the biology and management of shrubs. The first three were taxonomically oriented (Tiedemann and Johnson 1983; Tiedemann and others 1984; McArthur and Welch 1986); the fourth focused on animal relationships (Provenza and others 1987); and the fifth (this proceedings) has a physiological theme. The Shrub Research Consortium (see inside front cover of this proceedings) has sponsored these symposia as part of its role to facilitate the spread of knowledge of shrub biology and management. The Intermountain Research Station has published all five proceedings.

The presentations from this symposium are divided into three sections, Biotechnology and Breeding, Environmental Management and Technology, and Ecophysiology. The first section, Biotechnology and Breeding, examines some breeding system environmental response patterns of wildland shrubs (Pendleton and others; Sanderson and others), the tremendous potential for manipulation of plant species including wildland shrubs through the newly developing discipline of biotechnology (Carman), and application of some biotechnological techniques to one shrub, fourwing saltbush (*Atriplex canescens*) (Barrow; Wurtele). The second section, Environmental Management and Technology, examines vegetation establishment under a range of difficult conditions: Mohave Desert (both Romney and others papers), addition of polyacrylamide soil conditioners (Wallace and Wallace), and shrub community establishment in a northwestern riparian situation (Carson and Edgerton) and on reclaimed northeastern mine spoils (Hughes).

The third section, Ecophysiology, is the largest and most diverse. It includes papers covering a wide range of ecophysiological topics broadly divisible into water relations (Ansley and others; Booth; Carpenter and West; Ehleringer and Smedley; Sosebee and Wan), stress response and nutrition (Nelson and others; Nelson and Jolley, Rodriguez and Welch; Wallace, "Interaction..."), and processes (Meyer and Monsen; Noste and others; Stark; Wallace, "Comparative..."; Weber and others).

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A few of the papers presented (Shrub Research Consortium 1987) are not included in this proceedings. Notable among these was the last professional paper presented by Dr. Raymond B. Farnsworth (1915-1987), Emeritus Professor of Agronomy and Horticulture at Brigham Young University who served 14 years as chairman of that department and 2 years as Acting Dean of the College of Biology and Agriculture. Dr. Farnsworth (photo) is remembered as a caring teacher and administrator. He was particularly concerned and involved with increasing agricultural productivity among less technologically advanced peoples, including native Americans. His symposium paper, "Some Unanswered Problems Concerning Nitrogen Fixation in Shrub Ecosystems," dealt with a longstanding research interest of his on nitrogen fixation by nonlegume, semi-arid adapted plants (Farnsworth and Hammond 1968; Farnsworth and others 1976; Farnsworth 1987).



Raymond B.
Farnsworth

The symposium featured, in addition to the presented papers, a tour of laboratories of the Utah State University (USU) Biotechnology Center (Aust 1987) and a field tour to the Green Canyon field laboratory of the USU Ecology Center and the Intermountain Research Station Forestry Sciences Laboratory's plant physiology greenhouse. John Carman arranged and coordinated the biotechnology tour. The field tour was led by Martyn Caldwell and James Richards. It featured the ecophysiological (including grazing pressure) relationships of crested wheatgrass (*Agropyron desertorum*), bluebunch wheatgrass (*A. spicatum*), alfalfa (*Medicago sativa*), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), forage kochia (*Kochia prostrata*), and fourwing saltbush (*Atriplex canescens*) (Caldwell and others 1981; Caldwell 1984, 1985; Richards

and Caldwell 1985; Caldwell and Richards 1987; Pendery and Provenza 1987) and the drought tolerance of big sagebrush subspecies (Brown 1977; Welch and McArthur 1979; Brown and Collins 1980; McArthur 1983).

ACKNOWLEDGMENTS

We thank all members of the Shrub Research Consortium for their efforts in planning, publicizing, and conducting the symposium. In particular, we thank session discussion leaders D. Terrence Booth, Jerran T. Flinders, Marshall R. Haferkamp, and Fred D. Provenza. Kendall R. Johnson provided an instructive and delightful pair of slide-tape presentations at the banquet--"Moods of a Mountain" and the premier presentation of "Water on the Range." We also thank J. R. Goodin and Kevin R. Price for leading impromptu discussions on uses of biotechnology and remote sensing (Ridd and others 1984; Price 1987) in the resolution of shrub biology and management questions. We acknowledge others who helped with the symposium and its proceedings in various ways including Dee R. Funk and other staff of the USU Conference and Institute Division, Roberta L. Powell, and Nancy Clark.

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Section 1—Biotechnology and Breeding

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BREEDING SYSTEMS OF WOODY PLANT SPECIES IN UTAH //

Rosemary L. Pendleton, Burton K. Pendleton, and Kimball T. Harper

ABSTRACT: Breeding systems of all woody plant taxa listed in A Utah Flora were examined. A total of 351 species in 45 families were scored for floral, fruit, and growth characteristics, as well as ecological occurrence. A multivariate screening procedure was used to determine which variables best discriminate between monoecious, dioecious, polygamous, and perfect sexual systems. Pollen vector had the greatest influence, followed by woodiness and geographic occurrence for wind-pollinated species, and by height and flower color for animal-pollinated species. Factors affecting the evolution of these four sexual systems are discussed. Niche breadth was greater for dominant, wind-pollinated species and for wind- or bird-dispersed fruits. Optimal distance for gene flow apparently differs between ecological generalists and specialists.

INTRODUCTION

Plants exhibit an immense diversity of reproductive systems, ranging from completely selfing to obligate outcrossing, from bisexual flowers to unisexual individuals, and from monomorphic to trimorphic populations. Factors leading to the evolution of this diverse array have intrigued botanists since the mid-19th century (see Baker 1983). Historically, interest focused on the cataloguing of pollinators, arrangement of floral parts, and identification of pollination syndromes (Wyatt 1983). These syndromes refer to suites of morphological characters associated with definite pollen vectors such as wasp, hummingbird, moth, wind and others (Baker and Hurd 1968; Faegri and van der Pijl 1979; Proctor and Yeo 1973). Recently, the field of plant reproductive biology has experienced a resurgence of interest. The merging of traditional pollination biology with modern populations genetics has produced an experimentally based approach to breeding system evolution that currently receives much attention (Wyatt 1983).

Paper presented at the Symposium on Shrub Ecophysiology and Biotechnology, Logan, UT, June 30-July 2, 1987.

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Handel (1985) suggested three main components of plant breeding systems: 1) genetic recombination, including linkage and crossover, 2) pollination system, including pollen vector, outcrossing rate and arrangement of floral parts, and 3) dispersal of seeds. These three components set up patterns of gene flow within and between populations that are further modified by plant size (Dudash 1986; Handel 1985; Samson and Werk 1986), age (Floyd 1983; Lacey 1987), density (Handel 1983), and architecture (Webb and Lloyd 1986; Willson and Rathke 1974).

The optimal pattern of gene flow is dependent upon both biotic and abiotic components of the environment. Consequently, plant breeding systems must be viewed in an ecological context to be fully understood. Correlations between habitat and breeding system characteristics allow the identification of putative selective forces governing breeding system evolution. Several such correlation studies have previously been reported (Baker 1959; Bawa 1980; Collins 1983; Collins and others 1983; Fox 1985; Freeman and others 1980; Givnish 1980, 1982; Harper 1979; Muenchow 1987; Ostler and Harper 1978). Once identified, the role of putative factors can be examined critically through manipulative experimentation.

In this paper, we used plant morphology and habitat characteristics of the woody flora of Utah to examine broad trends in the ecological occurrence of reproductive systems and to compare our findings with those reported from other floras. We restrict the study to characteristics concerned with floral display, pollen vector, and seed dispersal. Information on outcrossing rates and genetic recombination is lacking for most of our native species. Specific questions addressed in this study are:

1. How does floral biology relate to plant morphology and ecology?
2. What ecological and morphological variables best discriminate between pollination systems?
3. Does relative abundance affect pollination system success?
4. Are ecological dominants more likely to be wind pollinated?
5. Is niche breadth greater for wind-pollinated species?
6. How is seed size related to means of dispersal?
7. Are pollen and seed dispersal mechanisms related?

METHODS

We surveyed all native woody plant species listed in Welsh and others' (1987) A Utah Flora. Plants were considered woody if described as suffrutescent, shrubby, or arboreous. Cacti and other succulents were also included. Suffrutescent species were not included in the study. A total of 351 species in 45 families were scored for the following 12 morphological and ecological characteristics:

1. Woodiness (succulent, subshrub, shrub, small tree, tree, vine).
2. Height class (0.25 m, 0.25-2.0 m, 2.0-8.0 m, 8.0 m).
3. Sexual system (monoecious, dioecious, polygamo-monoecious, polygamo-dioecious, perfect).
4. Pollen vector (wind, animal).
5. Fruit succulence (fleshy, dry).
6. Fruit dispersal type (megawind, bird, mammal, sticktight, dehiscent capsule, no apparent means).
7. Seed diameter class (1 mm, 2-3 mm, 4-5 mm, 6-8 mm, 9-12 mm, 13 mm).
8. Geographic occurrence (dominant, common, uncommon).
9. Canopy layer (overstory, understory, open).
10. Elevational range (100-m increments).
11. Number of counties in which species occurs.
12. Niche width (total of scores 10 and 11).

Animal-pollinated species were scored for the following additional characteristics:

13. Flower access (restricted, semi-restricted, unrestricted).
14. Flower color (green, white, yellow, pink, red, purple, blue, brown, black).
15. Flower symmetry (radial, bilateral).

Red spectrum (pink, red, orange) and blue spectrum (blue, purple) colors were each combined for statistical analysis. Polygamo-monoecious and polygamo-dioecious were similarly combined. Restricted flowers are defined as having a floral tube 3 mm in length and a throat opening of 1 cm. Semi-restricted flowers have a floral tube 3 mm or a throat 1 cm. Open (unrestricted) flowers lack a floral tube and allow free access to pollen and nectar. Classification of fruit dispersal type was based primarily on fruit morphology. References in the literature were also reviewed and incorporated.

Welsh and others (1987) was used as the primary source of information. Other sources included Arnow and others (1980) Flora of the Central Wasatch Front, Utah, Munz (1968) A California Flora, Kearney and Peebles (1960) Arizona Flora, McMin (1951) An Illustrated Manual of California Shrubs, and pressed specimens from the Brigham Young University herbarium (BRY). Geographic occurrence and canopy layer were scored subjectively by the authors. A complete listing of woody plant species and their scored characteristics is given in the Appendix.

Statistical Analysis

Preliminary analyses consisting of two-way contingency tables for sexual system against woodiness, height, pollen vector, fruit succulence, geographic occurrence, and canopy layer were carried out using the statistical package SPSS^x (SPSS Inc. 1983). This allowed us to compare our data with several other published studies, as well as to identify major trends. However, there are two major problems associated with this technique. First, observed correlations between two variables may actually be caused by their relationship to a third variable. For example, height, woodiness, and canopy layer are all highly intercorrelated. Second, although all have significant relationships, some variables may be more important (contain more information) than others. The use of multidimensional contingency tables circumvents the above two problems, but is sensitive with regard to empty cells and low expected values.

To determine which variables best discriminate between pollination systems, we used analysis of variance in a screening procedure somewhat analogous to backward stepwise regression. This procedure is one developed by Dr. Del T. Scott, Professor of Statistics, Brigham Young University, and is essentially a multivariate extension of the process described by Landis and Koch (1977). Use of this method allowed us to identify factors that remained significant while taking into account (controlling for) the other independent variables.

In the analysis, each sexual system (dioecious, monoecious, perfect, and polygamous) was treated as a separate dependent variable with levels of 1 and 0 for presence and absence, respectively. Woodiness, height, pollen vector, fruit succulence, geographic occurrence, canopy layer, flower color, symmetry, and access were all used as independent variables. A multivariate analysis of variance (General Linear Model) was carried out using the statistical package RUMMAGE available at Brigham Young University. Initially, all possible main effects and two-way interactions were examined. A completely saturated model, using higher order interactions, was not possible because of insufficient degrees of freedom. Following the initial run, variables and interactions with p values greater than 0.25 were omitted and the reduced model reanalyzed. This process was repeated until all factors left in the model were significant at or near the 0.05 level. Variables selected by the final model were examined more closely in chi-square contingency tables to determine trends with regard to pollination system.

The use of categorical data in an analysis designed for continuous variables requires some clarification. First, because the data are bivariate rather than continuous, small sample sizes may produce erratic results. Second, because the data represent the presence or absence of a particular trait, estimated values for group means become the percentage of total

species expressing that trait or combination of traits. Where empty cells exist, the program calculates pseudovalues that are used in estimating the group or cell mean. Results based upon pseudovalues must be viewed with caution.

Other analyses were carried out using the packages SPSS^x (SPSS Inc. 1983). SAS (SAS Institute Inc. 1982), or standard statistical procedures (Zar 1984). Data dealing with the effects of wind pollination, seed size, commonness, and dominance were examined by means of chi-square contingency tables. A General Linear Models (GLM) analysis of variance was run on niche breadth using pollen vector as the classification variable. The niche breadth variable was obtained by summing the elevational range and the number of counties in which the species occurred. Since the two variables had approximately the same spread, a straight rather than weighted sum was used. The resultant variable was then log transformed (Zar 1984) to normalize the data.

Where possible, statistical analyses were carried out at both the genus and species levels. Analysis at the species level allowed the retention of critical variation most closely associated with specific habitats. Analyses at the genus level minimized problems imposed by phylogenetic constraints, that is, retained characteristics due to recent shared ancestry. Domination of distribution patterns by a few speciose taxa can lead to the formation of false conclusions (Muenchow 1987). The database for genus-level analysis was obtained by selecting the first species listed alphabetically within each genus. For the most part, results reported in this paper will be from species-level analyses. Genus-level results will be reported only when they differ significantly from species-level results.

RESULTS

Sexual Systems

At the species level, dioecy was positively associated with a shrub or tree life form, increasing height, common geographic occurrence, and an overstory habit (table 1). Monoecy was associated with small (8 m) and large trees, increasing height, dry fruit, dominance, and an overstory habit. Polygamous species were associated with subshrubs, small stature, uncommon occurrence, and open habitat. Perfect-flowered species were associated with either succulents or shrubs, small stature, fleshy fruits, uncommon occurrence, and either open or understory habits. Identical relationships were found at the genus level with the exception of the fruit succulence variable. At the genus level, dioecy was correlated with fleshy fruits ($X^2 = 8.322$, $p = 0.040$) while perfect-flowered species showed no visible pattern.

Initial results from the screening procedure identified pollen vector as the single most important variable for describing sexual system. Wind pollination was associated with the dioecious or monoecious state; animal pollination was associated with perfect flowers ($X^2 = 144.73$, $p = 0.0001$). Similar results have been reported elsewhere (Freeman and others 1980; Givnish 1982; Muenchow 1987). Polygamy showed no bias toward either pollination system. Many of the trends reported in table 1 may be due to the association between sexual system and pollen vector. Trends reported for monoecy and dioecy were identical to those reported for wind pollination (table 2). Because of the great effect pollination vector has on sexual system, it seemed likely that other variables for discriminating between sexual

Table 1--Results from contingency table analyses for the association of sexual system with each of the variables listed below

	Woodiness	Height	Fruit ¹ succulence	Geographic occurrence	Canopy layer
Dioecious	Shrub, large tree	Tall	No trend	Common	Overstory
Monoecious	Small and large trees	Tall	Dry	Dominant	Overstory
Polygamous	Subshrub	Short	No trend	Uncommon	Open
Perfect	Succulent, shrub	Short	Fleshy	Uncommon	Open, understory
P value	NA ²	NA	0.0062	0.0000	0.0000

¹Results differed at the genus level.

²Chi-square statistics not applicable because of low expected values and empty cells.

Table 2--Results from contingency table analyses for the association of sexual system with each of the variables listed below

	Woodiness	Height	Fruit ¹ succulence	Geographic occurrence	Canopy layer
Wind	Small and large trees	Large stature	Dry	Dominant common	Overstory
Animal	Succulent, subshrub	Small stature	Fleshy	Uncommon	Open, understory
P value	0.0000	0.0000	0.0135	0.0000	0.0000

¹Results were nonsignificant at the genus level.

systems might differ between vector groups. In subsequent analyses, wind- and animal-pollinated species were run separately.

Wind pollination--The final model for wind-pollinated species contained the variables woodiness, geographic occurrence, and their interaction ($p = 0.000$, 0.000 , and 0.048 , respectively). This model best explained the overall (multivariate) difference between sexual systems. On a univariate basis, the model was most useful for describing monoecious and polygamous species (see adjusted R^2 values from table 3). Correlations between these two sexual systems and both the woodiness and geographic occurrence variables were observed. Dioecy was also somewhat correlated with the woodiness variable. No significant association between perfect-flowered species and the above variables was found.

The interaction term was significant only for polygamous species. When we graphed this interaction (fig. 1), we found that a high proportion of polygamous species occurred only at the subshrub and vine levels of woodiness. Lines drawn between these two levels would be parallel.

Table 3--Univariate results from analysis of variance screening procedure for wind-pollinated species. W = woodiness; G = geographic occurrence; WG = interaction term

	Adjusted R^2	P values		
		W	G	WG
Dioecious	0.074	0.056	0.147	0.576
Monoecious	0.252	0.002	0.052	0.982
Polygamous	0.423	0.000	0.000	0.000
Perfect	0.010	0.278	0.315	0.614

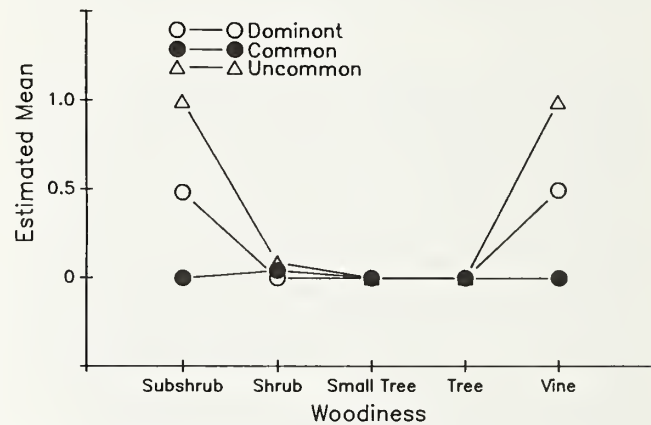


Figure 1--Estimated means from the woodiness-geographic occurrence interaction term for polygamous species.

The interaction term appears merely to reflect the lack of polygamous species at other levels of woodiness rather than any true interaction between the variables.

With the interaction term omitted, the effects of woodiness and geographic occurrence on sexual system could be examined directly through two-way contingency tables (tables 4, 5). Univariate statistics from the analysis of variance procedure were used to determine the significance of these relationships for each sexual system. Chi-square statistics were often of questionable value because of low expected values. The woodiness variable was significant for monoecy and polygamy, and nearly significant for dioecy (table 3). Monoecy was associated with small and large trees, while polygamy was overrepresented in the subshrubs (table 4). Dioecy appeared to be associated with the shrub habit. There was no pattern for perfect-flowered species. For geographic occurrence, monoecy occurred most often in dominant species, and polygamy in uncommon species (table 5). Dioecious and perfect-flowered species showed no significant trend.

Table 4--The relationship between woodiness and sexual system for wind-pollinated plant species (n = 88). The number of species exhibiting each combination of traits is listed above. Expected values are given in parentheses below

	Subshrub	Shrub	Small tree	Tree	Vine
Dioecious	- (1.13)	25 (19.88)	- (4.13)	7 (7.13)	1 (.075)
Monoecious	- (1.09)	11 (19.27)	9 (4.0)	12 (6.91)	- (0.73)
Polygamous	2 (0.20)	3 (3.61)	- (0.75)	- (1.30)	1 (0.14)
Perfect	1 (0.58)	14 (10.24)	2 (2.13)	- (3.67)	- (0.39)

Table 5--The relationship between geographic occurrence and sexual system for wind-pollinated plant species (n = 88). The number of species exhibiting each combination of traits is listed above. Expected values are given in parentheses below

	Geographic occurrence		
	Dominant	Common	Uncommon
Dioecious	4 (6.75)	17 (13.88)	12 (12.38)
Monoecious	13 (6.55)	10 (13.45)	9 (12.0)
Polygamous	- (1.23)	1 (2.52)	5 (2.25)
Perfect	1 (3.48)	9 (7.15)	7 (6.38)

At the genus level, woodiness and geographic occurrence were again the variables retained in the final model ($p = 0.006$ and 0.041 , respectively). Univariate relationships were significant at the 0.10 level for monoecy and polygamy versus woodiness ($p = 0.038$ and 0.001 , respectively) and for dioecy, monoecy, and polygamy versus geographic occurrence ($p = 0.093$, 0.016 , and 0.094 , respectively). Contingency tables show that monoecy was associated with both small and large tree life forms. Polygamy occurred only among subshrub or vine species. For geographic occurrence, dioecy occurred most often in common species, monoecy in dominant, and polygamy in uncommon species. Perfect-flowered species showed no significant trends.

Animal Pollination--The final model for animal-pollinated species contained the variables height, canopy layer, flower color, and the

color-canopy interaction term ($p = 0.017$, 0.000 , 0.000 , and 0.000 , respectively). Univariate results are given in table 6. This model best described dioecious and perfect-flowered species, as shown by the adjusted R-squared values. The significance of the monoecious terms is suspect because only four monoecious animal-pollinated species were included in the study. Results based on such a small sample size are of limited value, particularly when those results are expressed as percentages or proportions. The canopy layer and canopy-color interaction terms were significant only for monoecious species and can probably be eliminated from the model. Likewise, the significance of flower color in monoecious species will not be addressed.

We can now examine the effect of height and flower color on each sexual system. The variable height was significant only for dioecious species. The incidence of dioecy increased with height, going from 5.6 and 5.3 percent of the total species in categories 1 and 2 to 36.4 percent for category 3 and 100 percent of the total species in category 4. Floral color was significant for the dioecious and perfect floral systems. Dioecious species were predominantly green, or of the brown-black combination (table 7). Perfect-flowered species were mirror images, being underrepresented in the green, brown, or black colors and slightly overrepresented in the white or red-spectrum colors.

At the genus level, only the variable for flower color was retained in the final model. This variable was significant for dioecious and perfect species, and showed the same trend as that reported for the species level.

Niche Breadth and Geographic Occurrence

The following analyses dealt with questions of dominance and commonness, and their relation to means of pollen dispersal and sexual system. The preliminary contingency table analysis showed that dominant species were more likely to be pollinated by wind (table 2). This could be due

Table 6--Univariate results from analysis of variance screening procedure for animal-pollinated species

	Adjusted R^2	P values			
		Height	Canopy	Color	Color-canopy
Dioecious	0.627	0.001	0.217	0.000	0.417
Monoecious	0.199	0.832	0.000	0.000	0.000
Polygamous	0.000	0.368	0.532	0.416	0.722
Perfect	0.360	0.368	0.936	0.000	0.596

to a correlation between dominance and canopy layer. Dominant species were more likely to be found in the overstory ($X^2 = 41.1$, $p = 0.001$), and overstory species were often wind-pollinated and monoecious (see tables 2 and 4). To control for a possible canopy layer effect, we examined the relationship of pollen vector to dominance within each canopy layer. Dominant species were still more likely to be wind-pollinated in open habitat ($X^2 = 10.70$, $p = 0.001$), though not in the understory ($X^2 = 1.47$, $p = 0.48$). Uncommon taxa were more likely to be pollinated by animals ($X^2 = 30.23$, $p = 0.001$). They also tended to be perfect or polygamous ($X^2 = 27.33$, $p = 0.001$). This was true even when the effect of pollen vector was taken into account. No differences were found between common and uncommon species for flower symmetry, access, or color.

Breadth of ecological adaptation was further examined using the niche width variable. Niche breadth was wider in wind-pollinated species at both the species ($p = 0.0156$) and genus ($p = 0.027$) levels.

Seed Dispersal Mechanisms

Seed size correlated strongly with dispersal mechanism ($X^2 = 67.09$, $p = 0.001$). Although wind was important in every seed class category, seeds of 1 mm or less were almost exclusively dispersed by wind (table 8). Dehiscent capsules and sticktights were overrepresented in the 1-2 mm group. Fleshy fruits (generally bird dispersed) were overrepresented in the 3-5 mm group. Seeds greater than 6 mm were primarily mammal dispersed. Identical trends were observed at the genus level.

We also examined niche breadth as a function of seed dispersal system. Significant differences occurred between dispersal types at both genus ($p = 0.046$) and species ($p = 0.018$) levels. Bird and megawind dispersal types had the highest values for niche width. Mammal and sticktight dispersal types had the smallest.

Biotic and abiotic seed dispersal systems were compared with biotic and abiotic pollen

Table 7--The relationship between flower color and sexual system for animal-pollinated species. The number of species exhibiting each combination of traits is listed above. Expected values are given in parentheses below

	Flower color					
	Green	White	Yellow	Red	Blue	Brown/black
Dioecious	7 (1.3)	5 (10.6)	3 (9.0)	0 (3.3)	0 (2.3)	13 (1.4)
Monoecious	1 (0.2)	1 (1.5)	2 (1.3)	0 (0.5)	0 (0.3)	0 (0.2)
Polygamous	1 (0.7)	4 (5.7)	8 (4.8)	0 (1.8)	2 (1.3)	0 (0.7)
Perfect	3 (9.9)	90 (82.1)	72 (69.8)	31 (25.5)	20 (18.1)	1 (10.7)

Table 8--The relationship between seed size class and dispersal type. The number of species exhibiting each combination of traits is listed above. Expected values are given in parentheses below

	Seed size class (mm)			
	1	1-2	3-5	6
Wind	25 (13.4)	80 (70.4)	49 (60.5)	20 (29.7)
Dehiscent capsule or sticktight	1 (3.5)	27 (18.6)	10 (16.0)	8 (7.9)
Fleshy	0 (5.2)	25 (27.5)	35 (23.6)	8 (11.6)
Animal	1 (4.9)	10 (25.5)	28 (21.9)	24 (10.8)

Table 9--The relationship between abiotic or biotic pollen dispersal and seed dispersal. The number of species exhibiting each combination of traits is listed above. Expected values are given in parentheses below

	Pollen dispersal	
	Abiotic	Biotic
Seed Dispersal		
Abiotic		
Wind	62 (43.6)	112 (130.4)
Dehiscent capsule	0 (10.0)	40 (30.0)
Biotic		
Fleshy	10 (17.0)	58 (51.0)
Sticktight	16 (17.3)	53 (51.7)

dispersal. A chi-square test of the interdependence of pollen and seed dispersal systems was marginally significant ($X^2 = 4.44$, $0.025 < p < 0.05$). When dispersal system was broken down into types, however, the test was highly significant ($X^2 = 27.734$, $p < 0.001$) (see table 9).

DISCUSSION

The foregoing multivariate analyses were useful in determining which variables were most important in

distinguishing sexual systems of plants. While other techniques for multidimensional analysis of categorical data exist, problems with empty cells and low expected values precluded their use. Variables retained in our study contained information above and beyond that due to correlation with other variables. For example, dioecy was related to height beyond what could be accounted for by canopy layer, woodiness, or pollen vector. It is important to emphasize that while trends with other variables exist, those retained in the model contain equivalent information.

The genus- and species-level analyses gave similar results in almost all cases. Lower levels of significance were attained due to the smaller database, but trends remained the same. The only real exception was the fruit fleshiness variable, which was significantly associated with dioecy at the genus level but not at the species level. The overall similarity between the two levels of analysis indicates that phylogenetic constraints are not a major consideration for this flora, at least at the genus-species taxonomic level.

The variable having the greatest effect on floral system is pollen vector. Forces affecting flower morphology and inflorescence architecture for the two systems are radically different. Animal-pollinated species must attract their pollinators by means of visual signals, odor, nectar, or pollen. Flower morphologies vary widely, but are generally showy and have a large, conspicuously colored perianth. In contrast, wind-pollinated species need neither attract nor reward their pollen vector. In anemophilous species, floral parts can inhibit pollen dispersal. Flowers of wind-pollinated plants tend to be unisexual, have a perianth that is greatly reduced or lacking, and produce copious amounts of pollen (Faegri and van der Pijl 1979). Wind-pollinated species tend to flower early in the growing season before large-scale animal pollination begins and, more importantly, before deciduous species have leafed out. Leaves inhibit pollen flow (Whitehead 1983).

Wind pollination is a much less precise means of pollen transfer than animal-mediated pollination. Pollen transfer by wind is random within the context of prevailing winds. There is great potential for pollen wastage (Faegri and van der Pijl 1979; Richards 1986). Despite this drawback, wind pollination is important under certain environmental conditions and in certain geographic locations. On a large-scale basis, wind pollination increases with both elevation and latitude. It is uncommon in the tropics (Bawa 1980), but becomes the dominant means of pollination in northern deciduous and boreal forests (Whitehead 1969). Whitehead (1969) proposed a number of reasons for this pattern including the density and diversity of tropical floras, as well as existing weather patterns. Low temperature limits the activity of many animal pollinators, whereas rain greatly reduces the efficiency of wind pollination.

Wind pollination is common in the Intermountain region (Freeman and others 1980; McArthur, in press). Fully 25.1 percent of the woody plant species in Utah are pollinated by wind. Reasons for the high incidence of wind pollination in our region may be found by examining ecological correlates. Whitehead (1969, 1983) postulated conditions under which wind pollination will be effective. Wind pollination requires moderately dense vegetation of low diversity, or upper canopy status in more complex vegetation. A further requirement is the close spacing of compatible individuals. Since pollen transfer by wind has a large random component, the greater the proportion of compatible stigmas available in a given area, the more likely the chance of successful pollen transfer. Our results uphold Whitehead's ideas. We found wind pollination to be associated with tree life form, large stature, dry fruit, dominant or common occurrence, and an overstory canopy layer. Of these, life form (woodiness) and commonness of occurrence were the most efficient predictors of sexual system. Wind pollination was particularly associated with dominance. The Intermountain area is largely shrubland; large tracts of land are covered by low-growing dominants. Tree dominants reside as upper canopy species of more complex montane vegetation. These habitat conditions, coupled with the low level of rainfall, provide ideal situations for effective wind pollination.

Wind pollination has been implicated in the evolution of both monoecy and dioecy. We found wind pollination to be strongly correlated with these sexual systems. Nearly all monoecious plant taxa were pollinated by wind. Others have also found a correlation between wind and monoecy or dioecy in temperate zones (Freeman and others 1980; Muenchow 1987); a correlation not found in the tropics (Bawa 1980). The two primary reasons postulated for this correlation are the reduction of interference between male and female parts (Webb and Lloyd 1986) and a decrease in self-fertilization (Faegri and van der Pijl 1979). In wind-pollinated species, anthers and stigmas must be well-exposed to the wind in order for efficient pollination to occur. Separation of male and female parts likely enhances the dispersal of pollen. The separation of male and female parts into different flowers also reduces the amount of self pollen deposited on the stigma, increasing the opportunity for outcrossing. A substantial amount of self-fertilization can still occur, however, particularly as plant size increases. Wind-pollinated plants are often protogynous (Lloyd and Webb 1986), meaning stigmas are exerted before anthers on the same plant begin to dehisce. This greatly reduces the amount of self-fertilization. The separation of male and female parts into different individuals (dioecy) also overcomes this problem.

Freeman and his associates (1980) proposed a different reason for the correlation between wind pollination and dioecy. They proposed that dioecy evolved because of a differential success of male and female functions with microhabitat (see also Charnov 1982). Dioecy, in the region considered in their study, is associated with habitats where

there is substantial patchiness in soil moisture. Female plants are overrepresented on more mesic sites. Wind pollination, they state, appears to have preceded the evolution of dioecy and may facilitate its development because of potentially uneven gene flow patterns set up by wind pollination in patchy or heterogeneous environments. Uneven patterns of gene flow have been used by others in explanations regarding the evolution of dioecy (see Bawa 1980). Freeman and his associates (1980) further proposed that dioecy is associated with woodiness because of the increased selfing that accompanies larger plant size, which allows a rapid spread of genes coding for dioecy. In this study, we did find a slight increase of dioecy with plant size, irrespective of pollination system.

Animal pollination is much more common than pollination by wind. In this study, we found animal pollination significantly overrepresented in taxa that were small in stature, of uncommon occurrence, and were found either in the open or understory. The more specific transfer of pollen made possible by animal vectors allows efficient pollination even in understory positions or where individuals are widely spaced. Animal-pollinated species generally have perfect flowers, though a substantial portion of dioecious species also exist in that category.

The evolution of these dioecious animal-pollinated species poses an especially intriguing problem to botanists. We found dioecious animal-pollinated species to be correlated with increasing height and with inconspicuous (green or brown) flower color. Other studies have found correlations between dioecy and woodiness, fleshy fruit, and inconspicuous flowers (Bawa 1980; Fox 1985; Givnish 1980, 1982; Muenchow 1987). Fleshy fruit has been proposed as a causal agent in the evolution of dioecious animal-pollinated species. Muenchow (1987) found a slight association between dioecy and fleshy fruit, even when woodiness and flower color were controlled for in the analysis. We found no such association. Although an association was found between dioecy and fleshy fruit at the genus level in the initial contingency table analysis, this association disappeared in the presence of other variables. In her study, Muenchow suggested that constraints on both pollination and dispersal in the shrubby understory accounted for the association. Only one dioecious animal-pollinated understory shrub was included in our study.

The association between dioecy and woodiness has been interpreted as an increased need for outcrossing in long-lived taxa (see references in Bawa 1980). We also found dioecy to be specifically associated with height. Again, this could reflect the increase in self-fertilization associated with increasing plant size. We could also apply the argument of Freeman and others (1980), reported earlier, that genes coding for dioecy could spread more rapidly under self-fertilization.

The strongest association observed for animal-pollinated dioecious species was flower color. Others have reported strong correlations with inconspicuous flowers or unspecialized pollinators, both in tropic and temperate species (Bawa 1980; Fox 1985; Muenchow 1987). Restricted foraging patterns of small, unspecialized pollinators result in little pollen movement between genotypes. The evolution of dioecy can increase pollen flow between individuals. An alternative explanation involving sexual selection has also been proposed (see Bawa 1980 for a more complete discussion).

Unlike other sexual systems, polygamy was not associated with either pollination vector. The incidence of polygamous species was associated with small stature, particularly subshrubs, and with uncommon occurrence. Very little is known about the evolution of polygamous species. It has been suggested as an intermediate between perfect-flowered species and monoecy or dioecy (B. Charlesworth and D. Charlesworth 1978; D. Charlesworth and B. Charlesworth 1978) and, as such, is considered an outcrossing mechanism (Bawa and Beach 1981). The associations reported above, which differ markedly from those of dioecious and monoecious species, suggest some other role.

Polygamo-monoecy may provide savings in the allocation of resources between male and female floral parts. Many perfect-flowered species produce more flowers than can mature into fruit (Stephenson 1981). One role proposed for these "extra" flowers is to act as functional males. Andro-monoecy (the production of perfect and male flowers by one individual) is functionally equivalent, yet provides savings in resources normally allocated to female floral parts. Gyno-monoecy (the production of perfect and female flowers by one individual) is fairly common in the Compositae. Resources saved through the reduction of male floral parts may be reallocated to petals to enhance attractiveness to pollinators (Bawa and Beach 1981; Richards 1986).

Widely distributed species generally have larger populations, more continuous distribution and a greater potential for gene flow than geographically restricted species. Small isolated populations with restricted gene flow are characteristic of endemics (Hamrick and others 1979; Loveless and Hamrick 1984). We found geographically common species to be associated with wind pollination. Wind pollination was also associated with greater niche width. Animal pollination was associated with uncommon occurrence and with narrow niche width. Harper (1979) also reported an overrepresentation of animal pollination in rare or endangered species. Wind can disperse pollen over long distances (Richards 1986), thus increasing effective population size and resulting in high levels of genetic variability in outcrossing species (Hamrick and others 1979; Loveless and Hamrick 1984). High levels of variability may benefit species that experience a wide variety of environmental conditions, both between and within populations. Narrow endemics, which experience less ecological variability, also exhibit lower

levels of genetic variation (Hamrick and others 1979; Loveless and Hamrick 1984). Animal pollination (particularly bee pollination) results in more localized gene flow (Handel 1983; Richards 1986). In combination with small population size, this allows for a more structured population and fine-tuned genotypic adaptation (Waser and Price 1983).

Woodyness may play a part in the association between wind pollination, common occurrence, and increased genetic variability. Woody, long-lived perennials exhibit substantially more electrophoretic variation than herbaceous species (Hamrick and others 1979; Loveless and Hamrick 1984). Woody plants have slower maturation rates and so may have a slower rate of genetic fine-tuning to their environment. Also, taller species are subject to more extreme environmental conditions and may require a broader tolerance supplied through genetic heterogeneity.

Common or uncommon distribution patterns may be linked to floral morphology. Ostler and Harper (1978) found that locally uncommon species were more likely to have restricted access and zygomorphic flowers than were common species (see also Pendleton 1981). We found no difference between common and uncommon species with regard to floral access or symmetry. One reason for the differing results might be the different definitions for common and uncommon. We defined common on a geographic rather than a local basis. Common in a geographic sense is similar to niche width and reflects a broad adaptation. Common in a local sense reflects clumped spatial distribution. Harper (1979), however, did find geographically rare species to be associated with zygomorphic flower structure, though not with restricted access. Unlike Harper's study, our study focused on woody species only. Trends present in woody plant taxa sometimes differ from those present in the flora as a whole (Collins 1983; Ostler and Harper 1978).

Gene flow is also accomplished through the dispersal of seeds. A strong correlation was found between seed size and means of dispersal. This was not unexpected considering the different abilities of dispersal agents to transport mass. Van der Pijl (1982) reported a reduction in seed size for wind-dispersed fruits and commented on the ability of mammals to utilize large or heavy seeds. Dispersal agents that transport seeds farthest (birds, wind) were associated with greater niche width. Hamrick and his associates (1979) found greater, though nonsignificant, genetic variation in species dispersed by wind than in others. They did not differentiate bird-dispersed seeds. Wind is less efficient in dispersing seeds to specific habitats, but these species may have less specific habitat needs (see above). Dispersal by birds is more site-specific (Stiles 1987), yet birds are capable of transporting seeds for long distances. Birds and bird-dispersed fruits are more common in communities with complex vertical strata (Collins 1983). The correlation between bird-dispersed fruit and niche width may reflect, in part, the association between fleshy fruit and the tree

life form. As mentioned previously, trees exhibit a large amount of genetic variation and are considered to be generalists in habitat requirements.

Van der Pijl (1982) cautioned that pollen and seed dispersal are separate phenomena and should be examined independently. Nevertheless, we found a significant relationship between means of pollen dispersal and means of seed dispersal. Species having wind-dispersed seeds were also more likely to be pollinated by wind. Certainly, many of the constraints imposed on pollination by wind also apply to dispersal by wind. Wind dispersal should be most effective in open habitat or in canopy species or more complex vegetation. The capacity to exploit broad niches, as observed for dominant species, would also be compatible with the random nature of wind dispersal. Fleshy-fruited species were somewhat associated with animal pollination. Animal-pollinated species generally have a more restricted niche than wind-pollinated species. Birds are likely to disperse seeds to a habitat similar to that where they originated (Stiles 1987). Furthermore, understory species, which tend to be animal pollinated, are likely to be dispersed by wind. A clear exception to the overall correlation between pollination and dispersal was found in dehiscent capsules, which were exclusively animal pollinated. Capsules are multiple-seeded fruits and, as such, require animal pollination. Wind-pollinated species generally contain only one ovule per fruit (Faegri and van der Pijl 1979).

There are many other factors not mentioned here that affect plant breeding system. The degree of selfing versus outcrossing, incompatibility systems, and vegetative reproduction all affect gene flow. Also, temporal aspects of dispersal and flowering were not addressed.

Although a study of this kind cannot be inclusive, some implications for management can be drawn. Plants must be able to reproduce in place for long-term revegetation success. Species used for revegetation should be selected for their reproductive capabilities, as well as for vegetative growth characteristics. Wind-pollinated species should be planted as large continuous populations. Where wind pollination is predominate, species diversity should be kept low. Animal-pollinated species should be used in understory revegetation. Particular attention should be given to plants dependent on specialized animal pollinators to ensure that their pollination requirements are met. Several researchers have cautioned against the use of broad spectrum insecticides, particularly in areas of high species diversity or near populations of rare endemics (Harper 1979; Ostler 1976; Tepedino 1979).

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APPENDIX

Ecological and morphological characteristics of the woody plant species in Utah. Nomenclature follows Welsh and others' (1980) A Utah Flora. Characteristics are coded according to the

following key: (1) Woodiness; Sc = succulent, SS = subshrub, S = shrub, ST = small tree, T = tree, V = vine, (2) height; 1 = 0.25 m, 2 = 0.25-2.0 m, 3 = 2.0-8.0 m, 4 = 8.0 m, (3) sexual system; M = monoecious, D = dioecious, Po = polygamo-monoecious, PoD = polygamo-dioecious, P = perfect, (4) pollen vector; W = wind pollinated, A = animal pollinated, (5) fruit succulence; FL = fleshy, D = dry, (6) fruit dispersal; Fl = bird, A = mammal, DC = dehiscent capsule, St = sticktight, W = microwind, MW = megawind, N = no apparent means, (7) seed diameter; 1 = 1 mm, 2 = 2-3 mm, 3 = 4-5 mm, 4 = 6-8 mm, 5 = 9-12 mm, 6 = 13 mm, (8) geographic occurrence; D = dominant, C = common, U = uncommon, (9) canopy layer; O = overstory, U = understory, X = open habitat, (10) elevational range in 100-m increments, (11) number of counties in which the species occurs, (12) niche width; the sum of characters 10 and 11, (13) flower access; R = restricted, S = semi-restricted, O = unrestricted. See Methods section for a definition of these terms, (14) flower color; G = green, W = white, Y = yellow, P = pink, R = red, Pu = purple, Bl = blue, B = brown or black, and (15) flower symmetry; R = radial, B = bilateral. the latter three characteristics were scored only for animal-pollinated species. Vines were not scored for height.

	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
GYMNOSPERMAE															
Cupressaceae															
<u>Juniperus communis</u>	S	2	D	W	Fl	Fl	3	U	U	19	26	45			
<u>Juniperus osteosperma</u>	ST	3	M	W	Fl	Fl	4	D	O	16	28	44			
<u>Juniperus scopulorum</u>	T	3	D	W	Fl	Fl	3	C	O	14	28	42			
Ephedraceae															
<u>Ephedra fasciculata</u>	S	2	D	W	D	A	4	U	X	4	1	5			
<u>Ephedra nevadensis</u>	S	2	D	W	D	A	4	C	X	14	13	27			
<u>Ephedra torreyana</u>	S	2	D	W	D	A	4	C	X	15	9	24			
<u>Ephedra viridis</u>	S	2	D	W	D	A	4	U	X	22	18	40			
Pinaceae															
<u>Abies concolor</u>	T	4	M	W	D	W(A)	5	D	O	17	26	43			
<u>Abies lasiocarpa</u>	T	4	M	W	D	W	4	D	O	10	26	36			
<u>Picea engelmannii</u>	T	4	M	W	D	W	3	D	O	11	28	39			
<u>Picea pungens</u>	T	4	M	W	D	W	2	C	O	12	19	31			
<u>Pinus contorta</u>	T	4	M	W	D	W	3	D	O	14	6	20			
<u>Pinus edulis</u>	T	4	M	W	D	A	5	D	O	16	19	35			
<u>Pinus flexilis</u>	T	4	M	W	D	A	5	U	O	18	27	45			
<u>Pinus longaeva</u>	T	4	M	W	D	W(A)	4	C	O	12	14	26			
<u>Pinus monophylla</u>	T	4	M	W	D	A	6	D	O	18	11	29			
<u>Pinus ponderosa</u>	T	4	M	W	D	W(A)	4	D	O	12	21	33			
<u>Pseudotsuga menziesii</u>	T	4	M	W	D	W	3	D	O	17	28	45			
ANGIOSPERMAE															
Agavaceae															
<u>Agave utahensis</u>	Sc	3	P	A	D	DC	3	U	X	7	1	8	R	Y	R
<u>Nolina microcarpa</u>	S	2	D	A	D	W	3	U	X	1	1	2	O	W	R
<u>Yucca angustissima</u>	Sc	2	P	A	D	DC	5	U	X	17	8	25	O	W	R
<u>Yucca baccata</u>	Sc	2	P	A	Fl	A	5	C	X	17	5	22	O	W	R
<u>Yucca baileyi</u>	Sc	2	P	A	D	DC	4	C	X	11	4	15	O	W	R
<u>Yucca brevifolia</u>	ST	2	P	A	Fl	A	4	C	X	15	1	16	O	W	R
<u>Yucca harrimaniae</u>	Sc	2	P	A	D	DC	5	C	X	16	14	30	O	Y	R
<u>Yucca kanabensis</u>	Sc	2	P	A	D	DC	5	C	X	11	2	13	O	W	R
<u>Yucca schidigera</u>	S	2	P	A	Fl	A	4	U	X	7	1	8	O	W	R
<u>Yucca toftiae</u>	Sc	2	P	A	D	DC	4	U	X	8	3	11	O	W	R
<u>Yucca utahensis</u>	Sc	2	P	A	D	DC	4	C	X	11	1	12	O	W	R

(con.)

	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Aceraceae															
<u>Acer glabrum</u>	ST	3	M	A(W)	D	W	3	U	U	16	28	44	O	G	R
<u>Acer grandidentatum</u>	ST	3	M	W(A)	D	W	3	C	O	16	25	41			
<u>Acer negundo</u>	T	4	D	W	D	W	5	U	O	16	26	42			
Anacardiaceae															
<u>Rhus glabra</u>	ST	2	Po	A	F1	F1	3	U	X	13	10	23	O	G	R
<u>Rhus aromatica</u>	S	2	Po	A	F1	F1	3	C	O	16	26	42	O	Y	R
<u>Toxicodendron rydbergii</u>	S	1	D	A	F1	F1	3	U	O	13	17	30	O	W	R
Asteraceae															
<u>Acamptopappus sphaerocephalus</u>	S	2	P	A	D	W	2	C	X	6	3	9	S	Y	R
<u>Ambrosia dumosa</u>	S	2	M	W	D	ST	2	C	X	4	1	5			
<u>Ambrosia eriocentra</u>	S	2	M	W	D	ST	2	U	X	4	1	5			
<u>Amphipappus fremontii</u>	S	2	P	A	D	W	2	U	X	3	1	4	S	Y	R
<u>Artemisia arbuscula</u>	S	2	P	W	D	W	2	C	X	13	7	20			
<u>Artemisia bigelovii</u>	S	2	Po	W	D	W	2	U	X	12	10	22			
<u>Artemisia cana</u>	S	2	P	W	D	W	2	C	X	9	19	28			
<u>Artemisia filifolia</u>	S	2	M	W	D	W	1	C	X	16	8	24			
<u>Artemisia frigida</u>	S	1	P	W	D	W	2	U	X	27	21	48			
<u>Artemisia longiloba</u>	S	2	P	W	D	W	2	U	X	8	2	10			
<u>Artemisia nova</u>	S	1	P	W	D	W	2	C	X	13	22	35			
<u>Artemisia pygmaea</u>	S	1	P	W	D	W	2	U	X	8	12	20			
<u>Artemisia spiciformis</u>	S	2	P	W	D	W	2	U	X	5	10	15			
<u>Artemisia spinescens</u>	S	1	M	W	D	W	2	U	X	8	17	25			
<u>Artemisia tridentata</u>	S	2	P	W	D	W	2	C	X	20	28	48			
<u>Artemisia tripartita</u>	S	2	P	W	D	W	2	C	X	4	2	6			
<u>Baccharis emoryi</u>	S	2	D	W	D	MW	2	C	X	5	3	8			
<u>Baccharis glutinosa</u>	S	2	D	W	D	MW	2	C	X	5	2	7			
<u>Baccharis salicina</u>	S	2	D	W	D	MW	2	C	X	4	4	8			
<u>Baccharis sergilloides</u>	S	2	D	W	D	MW	2	U	X	2	1	3			
<u>Baccharis viminea</u>	S	3	D	W	D	MW	2	U	X	3	1	4			
<u>Baccharis wrightii</u>	S	2	D	W	D	MW	2	U	X	3	1	4			
<u>Bebbia juncea</u>	S	2	P	A	D	W	2	U	X	2	1	3	S	Y	R
<u>Brickellia atractylodes</u>	S	2	P	A	D	W	3	U	X	4	3	7	R	W	R
<u>Brickellia californica</u>	SS	2	P	A	D	W	3	U	X	14	11	25	S	W	R
<u>Brickellia longifolia</u>	S	2	P	A	D	W	2	U	X	9	7	16	S	W	R
<u>Brickellia microphylla</u>	S	2	P	A	D	W	3	U	X	16	15	31	S	W	R
<u>Brickellia oblongifolia</u>	SS	2	P	A	D	W	3	U	X	13	14	27	R	W	R
<u>Chrysothamnus albidus</u>	S	2	P	A	D	W	3	U	X	3	5	8	R	W	R
<u>Chrysothamnus depressus</u>	S	1	P	A	D	W	4	C	U	14	18	32	R	Y	R
<u>Chrysothamnus greenei</u>	S	2	P	A	D	W	3	C	X	15	13	28	S	Y	R
<u>Chrysothamnus linifolius</u>	S	2	P	A	D	W	2	U	X	15	12	27	S	Y	R
<u>Chrysothamnus nauseosus</u>	S	2	P	A	D	W	3	C	X	23	28	51	R	Y	R
<u>Chrysothamnus paniculatus</u>	S	2	P	A	D	W	2	C	X	6	1	7	R	Y	R
<u>Chrysothamnus parryi</u>	S	2	P	A	D	W	4	U	X	13	19	32	R	Y	R
<u>Chrysothamnus pulchellus</u>	S	2	P	A	D	W	3	U	X	11	3	14	R	Y	R
<u>Chrysothamnus vaseyi</u>	S	1	P	A	D	W	3	U	X	13	13	26	S	Y	R
<u>Chrysothamnus viscidiflorus</u>	S	2	P	A	D	W	3	C	U	20	28	48	S	Y	R
<u>Dyssodia acerosa</u>	SS	1	Po	A	D	W	3	U	X	4	3	7	R	Y	R
<u>Dyssodia pentachaeta</u>	SS	1	Po	A	D	W	2	U	X	6	1	7	S	Y	R
<u>Encelia farinosa</u>	S	2	P	A	D	W	3	U	X	1	1	2	S	Y	R
<u>Encelia frutescens</u>	S	2	P	A	D	W	4	U	X	11	5	16	S	Y	R
<u>Gutierrezia microcephala</u>	S	2	M	A	D	W	2	C	X	10	10	20	S	Y	R
<u>Gutierrezia petradoria</u>	SS	2	M	A	D	W	3	U	X	8	1	9	S	Y	R
<u>Gutierrezia pomariensis</u>	SS	2	Po	A	D	W	2	U	X	7	2	9	S	Y	R
<u>Gutierrezia sarothrae</u>	S	2	Po	A	D	W	2	C	X	17	28	45	S	Y	R
<u>Haplopappus cervinus</u>	S	2	P	A	D	W	2	U	X	8	2	10	S	Y	R
<u>Haplopappus crispus</u>	S	2	P	A	D	W	4	U	X	7	2	9	R	Y	R
<u>Haplopappus drummondii</u>	SS	2	P	A	D	W	2	U	X	8	5	13	S	Y	R
<u>Haplopappus laricifolius</u>	S	2	P	A	D	W	2	U	X	1	1	2	S	Y	R
<u>Haplopappus linearifolius</u>	S	2	P	A	D	W	3	U	X	8	1	9	R	Y	R
<u>Haplopappus macronema</u>	S	2	P	A	D	W	4	U	X	14	13	27	R	Y	R
<u>Haplopappus nanus</u>	S	1	P	A	D	W	3	U	X	16	7	23	S	Y	R

(con.)

	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<u>Haplopappus scopulorum</u>	S	2	P	A	D	W	3	U	U	5	4	9	S	Y	R
<u>Haplopappus watsonii</u>	S	2	P	A	D	W	3	U	X	22	10	32	S	Y	R
<u>Haplopappus zionis</u>	S	1	P	A	D	W	4	U	X	8	3	11	R	Y	R
<u>Hofmeisteria plurisetia</u>	S	2	P	W	D	W	2	U	X	4	1	5			
<u>Hymenoclea salsola</u>	S	2	M	W	D	W	3	U	X	3	1	4			
<u>Lepidospartum latisquatum</u>	S	2	P	A	D	W	2	U	X	1	1	2	S	Y	R
<u>Parthenium incanum</u>	S	2	M	A	D	W	2	U	X	1	1	2	S	W	R
<u>Perityle specuicola</u>	SS	2	P	A	D	W	3	U	X	2	2	4	S	W	R
<u>Perityle stansburyi</u>	SS	1	Po	A	D	W	3	U	X	7	8	15	S	Y	R
<u>Perityle tenella</u>	SS	1	P	A	D	W	3	U	X	13	1	14	S	Y	R
<u>Peucephyllum schottii</u>	S	2	P	A	D	W	3	U	X	1	1	2	S	Y	R
<u>Pluchea sericea</u>	S	2	Po	A	D	W	2	C	X	8	4	12	S	Pu	R
<u>Psilostrophe cooperi</u>	S	2	Po	A	D	W	4	U	X	13	1	14	S	Y	R
<u>Sphaeromeria diversifolia</u>	SS	2	Po	W	D	W	2	U	X	19	6	25			
<u>Sphaeromeria ruthiae</u>	SS	2	Po	W	D	W	2	U	X	8	1	9			
<u>Tetradymia axillaris</u>	S	2	P	A	D	W	3	U	X	6	1	7	R	Y	R
<u>Tetradymia canescens</u>	S	2	P	A	D	W	3	C	X	17	28	45	R	Y	R
<u>Tetradymia glabrata</u>	S	2	P	A	D	W	3	U	X	11	9	20	R	Y	R
<u>Tetradymia nuttallii</u>	S	2	P	A	D	W	3	U	X	5	9	14	R	Y	R
<u>Tetradymia spinosa</u>	S	2	P	A	D	W	4	U	X	7	15	22	R	Y	R
<u>Vanclevea stylosa</u>	S	2	P	A	D	W	3	C	X	6	6	12	R	Y	R
<u>Xylorhiza cronquistii</u>	SS	1	Po	A	D	W	3	U	X	3	1	4	R	W	R
<u>Xylorhiza glabriuscula</u>	SS	1	Po	A	D	W	3	U	X	7	3	10	S	W	R
<u>Xylorhiza tortifolia</u>	SS	2	Po	A	D	W	3	U	X	12	6	18	R	B1	R
Berberidaceae															
<u>Berberis fendleri</u>	S	2	P	A	F1	F1	3	U	X	8	2	10	O	Y	R
<u>Mahonia fremontii</u>	S	2	P	A	F1	F1(W)	3	C	X	17	6	23	O	Y	R
<u>Mahonia repens</u>	S	1	P	A	F1	F1	3	C	U	20	28	48	O	Y	R
Betulaceae															
<u>Alnus incana</u>	ST	3	M	W	D	W	3	C	O	15	15	30			
<u>Betula glandulosa</u>	S	2	M	W	D	W	2	U	O	8	6	14			
<u>Betula occidentalis</u>	ST	3	M	W	D	W	2	C	O	16	28	44			
<u>Ostrya knowltonii</u>	ST	3	M	W	D	W	4	U	O	6	3	9			
Bignoniaceae															
<u>Chilopsis linearis</u>	ST	3	P	A	D	W	4	U	O	8	1	9	R	W	B
Brassicaceae															
<u>Lepidium fremontii</u>	SS	2	P	A	D	W	2	U	X	9	1	10	O	W	R
Buddlejaceae															
<u>Buddleja utahensis</u>	S	2	P	A	D	DC	2	U	X	4	1	5	S	Y	R
Cactaceae															
<u>Coryphantha missouriensis</u>	Sc	1	P	A	F1	A	2	U	X	7	2	9	O	Y	R
<u>Coryphantha vivipara</u>	Sc	1	P	A	F1	A	2	U	X	14	14	28	O	P	R
<u>Echinocactus polycephalus</u>	Sc	2	P	A	D	A	3	U	X	3	2	5	R	Y	R
<u>Echinocereus engelmannii</u>	Sc	1	P	A	F1	F1	2	U	X	12	7	19	O	P	R
<u>Echinocereus triglochidiatus</u>	Sc	1	P	A	F1	F1	2	U	X	17	20	37	S	R	R
<u>Ferrocactus acanthodes</u>	Sc	2	P	A	D	A	2	U	X	7	1	8	O	Y	R
<u>Mammillaria tetrancistra</u>	Sc	1	P	A	F1	F1	2	U	X	6	1	7	O	R	R
<u>Neolloydia johnsonii</u>	Sc	1	P	A	D	A	2	U	X	6	1	7	O	Pu	R
<u>Opuntia acanthocarpa</u>	S	2	P	A	D	A	4	U	X	5	1	6	O	R	R
<u>Opuntia basilaris</u>	Sc	1	P	A	D	A	4	U	X	11	5	16	O	Pu	R
<u>Opuntia chlorotica</u>	S	2	P	A	F1	A	2	U	X	1	1	2	O	Y	R
<u>Opuntia echinocarpa</u>	S	2	P	A	D	A	2	U	X	7	2	9	O	Y	R
<u>Opuntia erinacea</u>	Sc	1	P	A	D	A	3	U	X	21	26	47	O	Y	R
<u>Opuntia fragilis</u>	Sc	1	P	A	D	A	4	U	X	13	15	28	O	Y	R
<u>Opuntia littoralis</u>	Sc	2	P	A	F1	A	3	U	X	1	2	3	O	Y	R
<u>Opuntia macrorhiza</u>	Sc	1	P	A	F1	A	3	U	X	12	7	19	O	Y	R
<u>Opuntia nicholii</u>	Sc	1	P	A	D	A	4	U	X	4	3	7	O	Pu	R
<u>Opuntia phaeacantha</u>	Sc	2	P	A	F1	A	3	U	X	12	4	16	O	Y	R
<u>Opuntia polyacantha</u>	Sc	1	P	A	D	A	3	C	X	16	28	44	O	Y	R
<u>Opuntia pulchella</u>	Sc	1	P	A	F1	A	3	U	X	5	4	9	O	Pu	R
<u>Opuntia whipplei</u>	Sc	2	P	A	F1	A	3	U	X	7	7	14	O	Y	R
<u>Pediocactus despainii</u>	Sc	1	P	A	D	A	3	U	X	1	1	2	O	Y	R
<u>Pediocactus sileri</u>	Sc	1	P	A	D	A	3	U	X	8	2	10	O	Y	R
<u>Pediocactus simpsonii</u>	Sc	1	P	A	D	A	2	U	X	14	19	33	O	W	R

(con.)

	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<u>Pediocactus winkleri</u>	Sc	1	P	A	D	A	3	U	X	2	1	3	O	P	R
<u>Sclerocactus pubispinus</u>	Sc	1	P	A	D	A	3	U	X	6	7	13	O	Y	R
<u>Sclerocactus whipplei</u>	Sc	2	P	A	D	A	2	U	X	14	10	24	O	P	R
<u>Sclerocactus wrightiae</u>	Sc	1	P	A	D	A	3	U	X	5	2	7	O	Y	R
Caprifoliaceae															
<u>Linnaea borealis</u>	SS	1	P	A	D	N	2	U	U	12	8	20	R	P	B
<u>Lonicera involucrata</u>	S	2	P	A	F1	F1	3	U	X	19	20	39	R	Y	B
<u>Lonicera utahensis</u>	S	2	P	A	F1	F1	3	U	U	17	12	29	R	Y	B
<u>Sambucus caerulea</u>	S	2	P	A	F1	F1	3	U	X	15	28	43	O	W	R
<u>Sambucus racemosa</u>	S	2	P	A	F1	F1	3	C	X	16	22	38	O	W	R
<u>Symphoricarpos longiflorus</u>	S	2	P	A	F1	F1	3	U	X	21	15	36	R	P	R
<u>Symphoricarpos occidentalis</u>	S	2	P	A	F1	F1	3	C	U	5	3	8	S	P	R
<u>Symphoricarpos oreophilus</u>	S	2	P	A	F1	F1	3	C	U	20	16	36	R	P	R
Caryophyllaceae															
<u>Arenaria macradenia</u>	SS	2	P	A	D	DC	2	U	X	22	11	33	O	W	R
Celastraceae															
<u>Forsellesia meionandra</u>	S	2	P	A	D	DC	3	U	X	9	9	18	O	W	R
<u>Forsellesia nevadensis</u>	S	2	P	A	D	DC	3	U	X	7	6	13	O	W	R
<u>Mortonia scabrella</u>	S	2	P	A	D	DC	3	U	X	5	1	6	O	W	R
<u>Pachystima myrsinites</u>	S	2	P	A	D	DC	3	C	U	16	28	44	O	R	R
Chenopodiaceae															
<u>Allenrolfea occidentalis</u>	S	2	P	W	D	W	1	C	X	3	15	18			
<u>Atriplex canescens</u>	S	2	D	W	D	W	2	C	X	18	23	41			
<u>Atriplex confertifolia</u>	S	2	D	W	D	W	2	D	X	13	25	38			
<u>Atriplex corrugata</u>	S	1	D	W	D	W	2	D	X	11	9	20			
<u>Atriplex gardneri</u>	S	2	D	W	D	W	2	D	X	10	20	30			
<u>Atriplex garrettii</u>	S	2	D	W	D	W	2	U	X	9	5	14			
<u>Atriplex hymenelytra</u>	S	2	D	W	D	W	2	U	X	1	1	2			
<u>Atriplex lentiformis</u>	S	2	D	W	D	W	2	C	X	3	1	4			
<u>Atriplex obovata</u>	S	2	D	W	D	W	2	C	X	3	1	4			
<u>Atriplex torreyi</u>	S	2	D	W	D	W	2	C	X	2	1	3			
<u>Ceratoides lanata</u>	S	2	M	W	D	W	2	D	X	22	23	45			
<u>Grayia spinosa</u>	S	2	M	W	D	W	2	C	X	22	18	40			
<u>Kochia americana</u>	SS	1	P	W	D	W	2	C	X	10	18	28			
<u>Sarcobatus vermiculatus</u>	S	2	M	W	D	W	2	D	X	11	26	37			
<u>Suaeda torreyana</u>	S	2	P	W	D	W	2	C	X	10	18	28			
<u>Zuckia brandegei</u>	S	2	M	W	D	W	2	C	X	12	9	21			
Cornaceae															
<u>Cornus sericea</u>	S	3	P	A	F1	F1	3	C	U	18	28	46	O	W	R
Elaeagnaceae															
<u>Elaeagnus commutata</u>	S	2	Po	A	F1	F1	4	C	X	7	2	9	O	Y	R
<u>Shepherdia argentea</u>	S	3	D	A	F1	F1	3	C	X	10	15	25	O	B	R
<u>Shepherdia canadensis</u>	S	2	D	W	F1	F1	3	U	U	13	17	30			
<u>Shepherdia rotundifolia</u>	S	2	D	W	F1	A	4	U	X	15	7	22			
Ericaceae															
<u>Arctostaphylos patula</u>	S	1	P	A	F1	A	3	C	U	15	18	33	R	P	R
<u>Arctostaphylos pringlei</u>	S	2	P	A	F1	F1	3	U	U	11	1	12	R	P	R
<u>Arctostaphylos pungens</u>	S	2	P	A	F1	F1	3	U	U	10	2	12	R	P	R
<u>Arctostaphylos uva-ursi</u>	S	1	P	A	F1	F1	3	C	U	15	9	24	R	P	R
<u>Gaultheria humifusa</u>	SS	1	P	A	F1	A	1	U	X	6	2	8	S	P	R
<u>Kalmia microphylla</u>	S	1	P	A	D	W	1	U	X	9	4	13	S	P	R
<u>Ledum glandulosum</u>	S	2	P	A	D	W	1	U	X	8	4	12	O	W	R
<u>Vaccinium caespitosum</u>	SS	1	P	A	D1	F1	2	C	U	13	8	21	R	P	R
<u>Vaccinium membranaceum</u>	S	2	P	A	F1	F1	2	D	U	7	6	13	R	P	R
<u>Vaccinium myrtillus</u>	S	1	P	A	F1	F1	2	U	U	12	5	17	S	P	R
<u>Vaccinium occidentale</u>	S	2	P	A	F1	F1	2	C	X	8	4	12	S	P	R
<u>Vaccinium scoparium</u>	SS	1	P	A	F1	F1	2	D	U	11	7	18	S	P	R
Fabaceae															
<u>Acacia greggii</u>	ST	3	P	A	D	A	4	C	O	1	1	2	O	G	R
<u>Caesalpinia gilliesii</u>	ST	3	P	A	D	A	3	U	O	5	4	9	R	P	B
<u>Parryella filifolia</u>	S	2	P	A	D	A	3	U	X	2	2	4	O	Y	R
<u>Prosopis glandulosa</u>	ST	3	P	A	D	A	4	C	X	6	1	7	O	G	R
<u>Prosopis pubescens</u>	ST	3	P	A	D	A	2	U	X	3	1	4	O	Y	R
<u>Psoralea arborescens</u>	S	2	P	A	D	A	3	U	X	4	1	5	R	B1	B
<u>Psoralea fremontii</u>	S	2	P	A	D	A	3	C	X	17	4	21	R	B1	B

(con.)

	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<u>Psorothamnus polydenius</u>	S	2	P	A	D	A	3	C	X	4	2	6	R	B1	B
<u>Psorothamnus thompsonae</u>	S	2	P	A	D	A	3	U	X	12	5	17	R	B1	B
<u>Robinia neomexicana</u>	ST	3	P	A	D	A	4	C	U	8	1	9	R	P	B
Fagaceae															
<u>Quercus eastwoodiae</u>	ST	3	M	W	D	A	6	U	X	8	4	12			
<u>Quercus gambelii</u>	ST	3	M	W	D	A	6	D	O	17	26	43			
<u>Quercus havardii</u>	S	2	M	W	D	A	6	C	X	2	6	8			
<u>Quercus pauciloba</u>	ST	3	M	W	D	A	6	U	X	9	10	19			
<u>Quercus turbinella</u>	S	2	M	W	D	A	6	D	O	10	3	13			
Garryaceae															
<u>Garrya flavescens</u>	S	2	D	W	F1	A	3	C	O	13	1	14			
Hydrophyllaceae															
<u>Eriodictyon argustifolium</u>	S	2	P	A	D	DC	2	C	X	15	1	16	S	W	R
Krameriaceae															
<u>Krameria grayi</u>	S	2	P	A	D	ST	3	U	X	6	1	7	O	Y	B
<u>Krameria parvifolia</u>	S	2	P	A	D	ST	4	U	X	4	1	5	O	Y	B
Lamiaceae															
<u>Poliomntha incana</u>	S	2	P	A	D	W	3	C	X	8	6	14	R	Pu	B
<u>Salazaria mexicana</u>	S	2	P	A	D	W	3	U	X	6	1	7	R	Pu	B
<u>Salvia dorii</u>	S	2	P	A	D	W	3	U	X	19	8	27	R	Pu	B
Loasaceae															
<u>Eucnide urens</u>	SS	2	P	A	D	W	1	U	X	3	1	4	O	Y	R
<u>Mentzelia shultzeorum</u>	SS	2	P	A	D	W	3	U	X	4	1	5	O	Y	R
<u>Petalonyx nitidus</u>	SS	2	P	A	D	DC	2	U	X	1	1	2	R	W	R
<u>Petalonyx parryi</u>	S	2	P	A	D	DC	2	U	X	2	1	3	R	W	R
Oleaceae															
<u>Forestiera pubescens</u>	S	2	D	W	F1	F1	3	C	X	8	5	13			
<u>Fraxinus anomala</u>	ST	3	P	W	D	W	5	U	X	18	9	27			
<u>Fraxinus velutina</u>	T	4	M	W	D	W	5	C	O	11	2	13			
<u>Menodora scabra</u>	SS	2	P	A	D	A	3	U	X	4	3	7	O	Y	R
<u>Menodora spinescens</u>	SS	2	P	A	D	A	3	U	X	2	1	3	R	W	R
Polemoniaceae															
<u>Gilia congesta</u> var.															
<u>frutescens</u>	SS	2	P	A	D	DC	2	U	X	12	4	16	R	W	R
<u>Gilia roseata</u>	SS	2	P	A	D	DC	3	U	X	12	6	18	R	W	R
<u>Leptodactylon pungens</u>	S	2	P	A	D	DC	2	C	X	14	18	32	R	W	R
<u>Leptodactylon watsonii</u>	SS	1	P	A	D	DC	2	U	X	20	12	32	R	W	R
<u>Linanthastrum nuttallii</u>	SS	1	P	A	D	DC	2	U	X	20	7	27	R	W	R
Polygalaceae															
<u>Polygala acanthoclada</u>	S	2	P	A	D	W	2	U	U	10	7	17	O	W	B
<u>Polygala subspinoso</u>	SS	1	P	A	D	W	3	U	U	11	13	24	O	P	B
Polygonaceae															
<u>Eriogonum bicolor</u>	S	1	P	A	D	W	2	U	X	8	7	15	O	W	R
<u>Eriogonum clavellatum</u>	S	1	P	A	D	W	2	C	X	5	1	6	S	W	R
<u>Eriogonum contortum</u>	S	1	P	A	D	W	2	U	X	3	1	4	O	Y	R
<u>Eriogonum corymbosum</u>	S	2	P	A	D	W	2	C	X	17	14	31	O	W	R
<u>Eriogonum fasciculatum</u>	S	2	P	A	D	W	2	C	X	9	1	10	O	W	R
<u>Eriogonum heermanni</u>	S	2	P	A	D	W	2	U	X	10	1	11	O	W	R
<u>Eriogonum heracleoides</u>	S	2	P	A	D	W	3	U	X	19	14	33	O	W	R
<u>Eriogonum leptocladon</u>	S	2	P	A	D	W	2	C	X	7	7	14	O	W	R
<u>Eriogonum leptophyllum</u>	S	2	P	A	D	W	3	U	X	1	1	2	O	W	R
<u>Eriogonum lonchophyllum</u>	S	2	P	A	D	W	2	U	X	9	3	12	O	W	R
<u>Eriogonum microthecum</u>	S	2	P	A	D	W	2	U	X	19	21	40	O	W	R
<u>Eriogonum nummulare</u>	S	2	P	A	D	W	2	U	X	10	5	15	O	W	R
<u>Eriogonum plumatella</u>	S	2	P	A	D	W	2	U	X	1	1	2	O	W	R
<u>Eriogonum thompsonae</u>	S	2	P	A	D	W	2	U	X	8	2	10	O	Y	R
<u>Eriogonum umbellatum</u>	SS	2	D	A	D	W	3	U	X	24	23	47	O	W	R
Pyrolaceae															
<u>Chimaphila menziesii</u>	SS	1	P	A	D	DC	1	U	U	1	1	2	O	W	R
Ranunculaceae															
<u>Clematis columbiana</u>	V		P	A	D	W	2	U	U	6	19	25	O	B1	R
<u>Clematis ligusticifolia</u>	V		D	A	D	W	2	U	O	14	23	37	O	W	R
<u>Clematis occidentalis</u>	V		P	A	D	W	2	U	U	8	7	15	O	B1	R
Rhamnaceae															
<u>Ceanothus fendleri</u>	S	2	P	A	D	DC	3	U	U	9	11	20	O	W	R
<u>Ceanothus greggii</u>	S	2	P	A	D	DC	3	U	U	18	5	23	O	W	R

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	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<u>Ceanothus martinii</u>	S	2	P	A	D	DC	3	U	U	12	17	29	O	W	R
<u>Ceanothus velutinus</u>	S	2	P	A	D	DC	2	D	O	11	13	24	O	W	R
<u>Rhamnus alnifolia</u>	S	2	D	W	F1	F1	3	U	X	1	2	3			
<u>Rhamnus betulifolia</u>	S	2	P	W	F1	F1	4	U	X	9	7	16			
Rosaceae															
<u>Amelanchier alnifolia</u>	ST	3	P	A	F1	F1	3	C	O	18	28	46	O	W	R
<u>Amelanchier utahensis</u>	S	3	P	A	F1	F1	3	C	O	20	28	48	O	W	R
<u>Cercocarpus intricatus</u>	S	2	P	W	D	W	3	U	X	11	17	28			
<u>Cercocarpus ledifolius</u>	ST	3	P	W	D	W	5	C	O	17	28	45			
<u>Cercocarpus montanus</u>	S	3	P	W	D	W	5	D	O	15	26	41			
<u>Chamaebatiaria millefolium</u>	S	2	P	A	D	W	3	U	O	15	11	26	O	W	R
<u>Coleogyne ramosissima</u>	S	2	P	A	D	A	3	D	X	11	7	18	O	Y	R
<u>Crataegus chrysocarpa</u>	ST	3	P	A	F1	F1	4	U	O	1	1	2	O	W	R
<u>Crataegus douglasii</u>	ST	3	P	A	F1	F1	3	C	U	11	20	31	O	W	R
<u>Crataegus succulenta</u>	ST	3	P	A	F1	F1	4	U	O	3	1	4	O	W	R
<u>Dryas octopetala</u>	S	1	P	A	D	W	2	C	X	6	4	10	O	W	R
<u>Fallugia paradoxa</u>	S	2	D	A	D	W	2	C	X	15	7	22	O	W	R
<u>Holodiscus dumosus</u>	S	2	P	A	D	W	2	U	X	24	28	52	O	W	R
<u>Peraphyllum ramosissimum</u>	S	2	P	A	F1	A	3	U	X	11	13	24	O	P	R
<u>Petrophytum caespitosum</u>	SS	1	P	A	D	DC	2	U	X	21	18	39	O	W	R
<u>Physocarpus alternans</u>	S	2	P	A	D	DC	2	U	X	9	16	25	O	W	R
<u>Physocarpus malvaceus</u>	S	2	P	A	D	DC	2	D	U	18	13	31	O	W	R
<u>Physocarpus monogynus</u>	S	2	P	A	D	DC	2	U	U	6	2	8	O	W	R
<u>Potentilla fruticosa</u>	S	2	P	A	D	A	2	C	U	19	23	42	O	Y	R
<u>Prunus americana</u>	S	3	P	A	F1	F1	6	U	X	5	8	13	O	W	R
<u>Prunus emarginata</u>	ST	3	P	A	F1	F1	4	U	U	1	1	2	O	W	R
<u>Prunus fasciculata</u>	S	2	PoD	A	D	A	4	C	X	13	4	17	O	W	R
<u>Prunus virginiana</u>	ST	3	P	A	F1	F1	4	C	O	18	28	46	O	W	R
<u>Purshia glandulosa</u>	S	2	P	A	D	A	3	D	X	4	1	5	O	Y	R
<u>Purshia mexicana</u>	ST	3	P	A	D	W	3	C	X	18	19	37	O	W	R
<u>Purshia tridentata</u>	S	2	P	A	D	A	3	C	X	17	28	45	O	Y	R
<u>Rosa nutkana</u>	S	2	P	A	F1	F1	3	U	U	20	26	46	O	P	R
<u>Rosa woodsii</u>	S	2	P	A	F1	F1	3	U	U	26	28	54	O	P	R
<u>Rubus idaeus</u>	S	2	P	A	F1	F1	2	U	X	14	28	42	O	W	R
<u>Rubus leucodermis</u>	S	2	P	A	F1	F1	2	U	U	11	7	18	O	W	R
<u>Rubus neomexicanus</u>	S	2	P	A	F1	F1	2	U	X	2	1	3	O	W	R
<u>Rubus parviflorus</u>	S	2	P	A	F1	F1	2	U	U	14	14	28	O	W	R
<u>Sorbus scopulina</u>	S	3	P	A	F1	F1	3	U	U	9	13	22	O	W	R
Rubiaceae															
<u>Galium multiflorum</u>	SS	2	D	A	D	ST	2	U	X	17	21	38	S	Y	R
<u>Galium stellatum</u>	S	2	D	A	D	ST	2	U	X	3	1	4	S	Y	R
Rutaceae															
<u>Ptelea trifoliata</u> ssp.															
<u>pallida</u>	ST	3	PoD	A	D	W	4	U	X	4	3	7	O	W	R
<u>Thamnosma montana</u>	S	2	P	A	D	A	3	C	U	6	2	8	S	Pu	R
Salicaceae															
<u>Populus acuminata</u>	T	4	D	W	D	MW	2	C	O	6	15	21			
<u>Populus angustifolia</u>	T	4	D	W	D	MW	2	C	O	10	28	38			
<u>Populus balsamifera</u>	T	4	D	W	D	MW	2	C	O	11	7	18			
<u>Populus fremontii</u>	T	4	D	W	D	MW	2	C	O	12	15	27			
<u>Populus tremuloides</u>	T	4	D	W	D	MW	2	D	O	19	28	47			
<u>Salix amygdaloides</u>	ST	3	D	A(W)	D	MW	1	C	O	7	15	22	O	G	R
<u>Salix arctica</u>	S	1	D	A(W)	D	MW	1	U	X	9	7	16	O	B	R
<u>Salix bebbiana</u>	S	3	D	A(W)	D	MW	1	U	X	14	19	33	O	G	R
<u>Salix boothii</u>	S	3	D	A(W)	D	MW	1	U	X	11	20	31	O	B	R
<u>Salix brachycarpa</u>	S	2	D	A(W)	D	MW	1	U	X	12	14	26	O	G	R
<u>Salix cascadiensis</u>	SS	1	D	A(W)	D	MW	1	U	X	6	4	10	O	B	R
<u>Salix drummondiana</u>	S	3	D	A(W)	D	MW	1	U	X	13	16	29	O	B	R
<u>Salix exigua</u>	S	3	D	A(W)	D	MW	1	C	X	19	28	47	O	G	R
<u>Salix geyeriana</u>	S	3	D	A(W)	D	MW	1	C	O	8	16	24	O	B	R
<u>Salix glauca</u>	S	2	D	A(W)	D	MW	1	C	O	10	8	18	O	B	R
<u>Salix gooddingii</u>	T	4	D	A(W)	D	MW	1	C	O	9	5	14	O	G	R
<u>Salix laevigata</u>	T	4	D	A(W)	D	MW	1	C	O	8	3	11	O	Y	R
<u>Salix lasiandra</u>	ST	3	D	A(W)	D	MW	1	C	O	12	23	35	O	G	R
<u>Salix lasiolepis</u>	ST	3	D	A(W)	D	MW	1	C	O	9	9	18	O	B	R
<u>Salix lutea</u>	S	3	D	A(W)	D	MW	1	C	O	12	23	35	O	B	R

(con.)

	Characteristic														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<u>Salix monticola</u>	S	3	D	A(W)	D	MW	1	C	X	11	8	19	O	B	R
<u>Salix planifolia</u>	S	2	D	A(W)	D	MW	1	C	U	15	10	25	O	B	R
<u>Salix reticulata</u>	S	1	D	A(W)	D	MW	1	U	X	11	7	18	O	G	R
<u>Salix scouleriana</u>	ST	3	D	A(W)	D	MW	1	U	U	21	22	43	O	B	R
<u>Salix wolfii</u>	S	2	D	A(W)	D	MW	1	U	X	9	7	16	O	B	R
Saxifragaceae															
<u>Fendlera rupicola</u>	S	2	P	A	D	DC	4	U	X	4	2	6	O	W	R
<u>Fendlera utahensis</u>	S	2	P	A	D	DC	2	U	X	14	6	20	O	W	R
<u>Jamesia americana</u>	S	2	P	A	D	DC	2	U	X	21	5	26	O	W	R
<u>Phyladelphus microphyllus</u>	S	2	P	A	D	DC	2	U	X	16	16	32	O	W	R
<u>Ribes aureum</u>	S	3	P	A	F1	F1	3	C	X	14	26	40	R	Y	R
<u>Ribes cereum</u>	S	2	P	A	F1	F1	2	C	X	19	27	46	R	W	R
<u>Ribes hudsonianum</u>	S	2	P	A	F1	F1	2	U	X	9	6	15	O	W	R
<u>Ribes inerme</u>	S	2	P	A	F1	F1	2	U	X	14	18	32	S	W	R
<u>Ribes lacustre</u>	S	2	P	A	F1	F1	2	U	X	14	4	18	O	Pu	R
<u>Ribes laxiflorum</u>	S	2	P	A	F1	F1	2	U	X	3	1	4	O	Pu	R
<u>Ribes leptanthum</u>	S	2	P	A	F1	F1	2	U	X	9	7	16	S	W	R
<u>Ribes montigenum</u>	S	2	P	A	F1	F1	2	C	U	17	24	41	O	Pu	R
<u>Ribes setosum</u>	S	2	P	A	F1	F1	3	U	X	8	4	12	R	W	R
<u>Ribes velutinum</u>	S	2	P	A	F1	F1	2	C	X	10	5	15	S	W	R
<u>Ribes viscosissimum</u>	S	2	P	A	F1	F1	3	U	U	10	16	26	R	W	R
<u>Ribes wolfii</u>	S	2	P	A	F1	F1	2	U	X	19	11	30	S	W	R
Scrophulariaceae															
<u>Penstemon ambiguous</u>	SS	2	P	A	D	DC	2	U	X	13	5	18	R	P	B
<u>Penstemon caespitosus</u>															
var. <u>suffruticosus</u>	SS	1	P	A	D	DC	2	U	X	10	5	15	R	B1	B
<u>Penstemon deustus</u>	SS	1	P	A	D	DC	2	U	X	8	1	9	R	W	B
<u>Penstemon petiolatus</u>	SS	1	P	A	D	DC	2	U	X	16	1	17	R	B1	B
<u>Penstemon linarioides</u>	SS	1	P	A	D	DC	2	U	X	5	4	9	R	P	B
Solanaceae															
<u>Lycium andersonii</u>	S	2	P	A	F1	F1	2	C	X	15	8	23	R	W	R
<u>Lycium cooperi</u>	S	2	P	A	F1	F1	2	U	X	4	1	5	R	W	R
<u>Lycium pallidum</u>	S	2	P	A	F1	F1	2	U	X	10	5	15	R	G	R
<u>Lycium torreyi</u>	S	2	P	A	F1	F1	2	U	X	5	2	7	R	Pu	R
Ulmaceae															
<u>Celtis reticulata</u>	ST	3	M	W	F1	F1	3	U	O	7	16	23			
Verbenaceae															
<u>Aloysia wrightii</u>	S	2	P	A	D	W	2	U	X	1	1	2	S	W	B
Vitaceae															
<u>Parthenocissus vitaceae</u>	V		Po	W	F1	F1	3	U	O	3	3	6			
<u>Vitis arizonica</u>	V		PoD	W	F1	F1	3	C	O	6	1	7			
Zygophyllaceae															
<u>Larrea tridentata</u>	S	2	P	A	D	W	3	D	O	5	1	6	O	Y	R

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A RELATIONSHIP BETWEEN POLYPLOIDY AND HABITAT IN WESTERN SHRUB SPECIES

Stewart C. Sanderson, E. Durant McArthur, and Howard C. Stutz

ABSTRACT: The relationships between polyploidy and physiological stress and polyploidy and the gigas syndrome were re-examined by considering data from western wildland shrubs. In general, these shrubs give renewed credence to Hagerup's Hypothesis (for at least some situations) that polyploids are better adapted to ecologically stressful environments than their diploid relatives. In contrast to the traditional gigas syndrome associated with the polyploid state of herbaceous plants, the shrubs Artemisia tridentata, Atriplex canescens, A. confertifolia, and Chrysothamnus viscidiflorus are more robust as diploids. A lower rate of cell division and growth has generally been observed for polyploid tissues, and may be selectively advantageous where moisture supplies are insufficient for the support of taller statures. However, a U-shaped curve for plant height was observed over a larger range of ploidies (2x-10x) available in A. confertifolia in Western Utah. While diploids in this area were located on well-drained slopes, polyploid populations occurred on saline lowlands, often with higher water tables. Measurements of electrical conductivity of soils and of leaf extracts for these populations suggest an increase of osmotic capability with ploidy.

INTRODUCTION

This study and accompanying review were undertaken because we have observed that some western shrub genera, notably Artemisia and Atriplex, have giant diploid forms that are adapted to more mesic habitats, in general, than many of their polyploid relatives (Stutz and others 1975; Stutz and Sanderson 1979, 1983; Barker and McKell 1981; McArthur and others 1981; McArthur and Welch 1982; Dunford 1984). We felt this information would have some bearing on a longstanding controversy on physiological adaptation of the polyploid state. Hagerup (1932) suggested that polyploids were better adapted to extreme ecological environments than were their diploid relatives. This

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hypothesis has been supported by investigators and reviewers of several taxa over a broad geographical range (Tischler 1935, 1937; Wulff 1937; Löve and Löve 1943, 1957; Johnson and Packer 1965). On the other hand, Bowden (1940), Gustafsson (1948), Stebbins (1950, 1971), and Powell and Sloan (1975) have opposed Hagerup's Hypothesis in favor of an alternate suggestion by Stebbins (1950) that increasing polyploid frequencies have resulted from a selective advantage of highly heterozygous polyploids in unstable environments. In recent reviews both Grant (1971) and Lewis (1980) recognized the validity of Stebbins' Hypothesis that increased polyploid frequencies do result from unstable environments but both reviewers also acknowledged possible merit in Hagerup's Hypothesis especially as championed by the Löves. It has been shown conclusively that both diploid and polyploid species can have broad ecological adaption (Stebbins 1971)--Hancock and Bringham's 1978 and 1979 examples of diploid and octoploid Fragaria species, respectively, are illustrative.

In this paper we: (1) briefly review the relationship between polyploidy and habitat of several western wildland shrub species adapted to semi-arid conditions, and (2) present stature, water status, and other measurements for two species (Artemisia tridentata and Atriplex confertifolia) each of which have contiguous diploid and polyploid populations and for which we have studied chromosome number distribution (McArthur and others 1981; Stutz and Sanderson 1983; McArthur and Sanderson 1987). We consider relationships between habitat, ploidy, and growth habit. We were particularly interested in the distribution of giant (gigas) growth habit. The gigas habit has been best characterized in herbaceous plants and attributed as a function of polyploidy (Smith 1946; Solbrig 1971; Lewis 1981). However, in earlier publications (Stutz and others 1975; McArthur and Welch 1982; Stutz and Sanderson 1983) we presented evidence that some western wildland shrubs have a more robust form associated with diploidy.

Artemisia tridentata ssp. wyomingensis (tetraploid) is a shrub of arid valley slopes and is usually 3 feet in height or less, while A. t. tridentata (diploid) which grows adjacent to arroyos and in other locations of higher moisture availability has been measured as much as 15.6 feet in height (McArthur and Welch 1982). Monsen and McArthur (1985) documented a lower level of annual precipitation for ssp. wyomingensis (34.8 ± 2.3 cm.) than for ssp. tridentata (45.3 ± 3.6 cm.). Atriplex canescens diploids, which are found chiefly in sandy situations, are mostly

taller than tetraploids (Stutz and others 1979). Diploids of Atriplex confertifolia are found elevationally higher and are generally taller than tetraploids (Stutz and Sanderson 1983).

Data available for polyploid western shrub taxa suggest that as a generality diploids are larger and grow in more mesic habitats than do related polyploids (table 1). In six of the 10 taxa (Ambrosia dumosa, Artemisia tridentata, Atriplex

canescens, A. confertifolia, Chrysothamnus viscidiflorus, Larrea tridentata) diploids are adapted either on local or regional scales to more mesic habitats than are polyploids. The other four taxa listed in table 1 (Arctostaphylos spp., Grayia brandegei, Gutierrezia sarothrae, Sarcobatus vermiculatus) apparently do not follow ploidy/moisture gradients although Sarcobatus includes a diminutive species, S. baileyi, which is a high polyploid and grows on more xeric sites

Table 1--Generalized ploidy, growth habit, and habitat relationships in some western wildland shrubs

Taxon	Chromosome races			References
	Ploidy	Growth habit	Habitat preference	
<u>Ambrosia dumosa</u> x = 18 ²	2x	-- ¹	widespread	Raven and others 1969
	4x	--	widespread	
	6x	--	widespread	
<u>Arctostaphylos</u> spp. x = 13	2x	--	variable	Wells 1968
	4x	--	variable	
<u>Artemisia tridentata</u> ³ x = 9	2x	large	mesic	McArthur and Welch 1982; Barker and McKell 1983, 1986; this paper
	4x	smaller	drier	
<u>Atriplex canescens</u> x = 9	2x	largest	mesic	Stutz and others 1975; Stutz and Sanderson 1979; Dunford 1984, 1985
	4x	smaller	drier	
	6x	smallest	drier	
	12x	smaller	driest	
<u>Atriplex confertifolia</u> x = 9	2x	large	mesic	Stutz and Sanderson 1983; this paper
	4x	variable	drier	
	6x	variable	saline	
	8x	variable	saline	
	10x	largest	saline	
<u>Chrysothamnus viscidiflorus</u> x = 9	2x	largest	dry	Anderson 1986
	4x	smaller	drier	
	6x	smallest	driest	
<u>Grayia brandegei</u> x = 9	2x	smaller	restricted	Stutz and others 1987
	4x	larger	wider	
<u>Gutierrezia sarothrae</u> x = 4	2x	smaller	mixed 2x-4x populations	Solbrig 1977
	4x	larger	mixed 2x-4x populations	
<u>Larrea tridentata</u> x = 13	2x	--	dry	Yang 1970; Hunziker and others 1977
	4x	--	drier	
	6x	--	driest	
<u>Sarcobatus</u> ² <u>vermiculatus</u> x = 18 ²	4x	--	northern	Roos 1984
	6x	--	southern	

¹Indicates no data available or no detectable differences between ploidy levels.

²Base number is probably x = 9 but no diploids at that level have been discovered.

³Taxon includes four subspecies. For details see McArthur and others 1979 and Goodrich and others 1985. 6x populations reported by McArthur and others (1981) are an undescribed stabilized hybrid between A. tridentata and A. arbuscula (Winward and others 1986).

than does S. vermiculatus (Stutz 1987). The large stature-diploid syndrome of western wildland shrubs clearly includes Artemisia tridentata, Atriplex canescens, A. confertifolia, and Chrysothamnus viscidiflorus. It is suggested that a lowering of growth in polyploid shrubs, allowing an increased ability to survive in situations of limited soil moisture, has allowed the origin of drought-resistant forms from a more mesically adapted diploid ancestry.

Further evidence for such a diploid/mesic habitat interpretation comes from Artemisia and Atriplex congeners growing in Eurasia and Australia, respectively. Artemisia santonicum has fast-growing diploids and slower growing polyploids (Persson 1974). Atriplex vesicaria includes diploid, tetraploid, and hexaploid chromosome races (Nobs 1980) and populations of differential stature (Parr-Smith and Calder 1979) although the ploidy/growth habit correlations have not been made. That the tall and fast growth rate of diploids has a strong genetic component is demonstrated in common garden studies (Stutz and others 1975; McArthur and Welch 1982; McArthur and others 1983; Jones and others 1987). Clear exceptions to the giant diploid syndrome are Grayia brandegei and Gutierrezia sarothrae (table 1). In both of these cases tetraploids are larger than diploids. We believe it is interesting that these species are more nearly herbaceous, with which growth form the gigas polyploid syndrome has traditionally been associated. Grayia brandegei and Gutierrezia sarothrae are suffrutescent shrubs, the latter with close herbaceous relatives (McArthur and others 1979; Solbrig 1977). Suffrutescent Atriplex ssp. (A. gardeneri complex), studied by Pope (1976) and Stutz and others (1979) but not included in table 1 have larger diploids of mesic habitat for some phylogenetic lines but not others (Stutz and Sanderson 1986).

MATERIALS AND METHODS

At individual study sites, healthy mature plants were randomly selected for study. Data collected included shrub heights (cm) and pressure bomb measurements (MPa) of shrub twig water potentials (Waring and Cleary 1967; Freeman and McArthur 1982). Water potential data were collected during the afternoons of the week of September 21, 1987 after a period of several weeks without rain. Skies were sunny or had high, thin clouds on each day of measurement.

Water potential measurements at Artemisia tridentata sites were made by alternately measuring a plant of one ploidy level and then one of the other. Artemisia tridentata was examined at two locations, at one-half mile west of Sage, Lincoln County, and at the north foot of South Table Mountain, Sweetwater County, in Wyoming, on September 25 and 26, 1987, respectively. The diploid plants in this study were A. tridentata ssp. tridentata whereas the tetraploid ones were A. tridentata ssp. wyomingensis. The subspecies have differences but are closely related and share a common

karotype (McArthur and others 1979, 1981; McArthur and Welch 1982).

Atriplex confertifolia ploidy races did not occur sympatrically and therefore sites with different ploidy levels in a given area were sampled sequentially. At the first, Rush Valley, 10 individuals were measured for each ploidy level, and afterwards the sites were revisited in the same sequence and 10 more individuals measured. No observable change occurred, therefore due to constraints of time and distance, measurement at the other two A. confertifolia areas were made for 20 individuals per site on single visits. Measurements for the three A. confertifolia areas were made on separate days. These were Rush Valley, Tooele Co., Skull Valley, Tooele Co., and Snake Valley, Millard Co., Utah, on September 22, 23, and 24, 1987. Diploids of the three series were located near the respective valleys at Fivemile Pass (for Rush Valley), Hastings Pass (for Skull Valley), and the U.S. Highway 6 Confusion Range Summit (for Snake Valley).

Measurements of soil properties (electrical conductivity, texture, pH) (Black 1968) and indication of depth of the water table (Kearney and others 1914; Roos 1984) were collected for each A. confertifolia site (table 2). Electrical conductivity measurements were made of leaf tissue of A. confertifolia (table 3) from the Snake Valley populations. Leaves were oven dried at 40 °C, ground, and 0.1 g samples were further ground in a mortar and pestle with 2 ml water and centrifuged. Fifty microliters of the supernatant were diluted with 3 ml of water, giving a ratio of 0.83 mg leaf weight per ml solution.

Statistical analyses were performed using SAS analysis of variance (ANOVA) followed when appropriate by the Student-Newman-Kuels multiple range means comparison tests (SNK) (SAS Institute 1985).

RESULTS

As in previous reports (McArthur and others 1979; McArthur and Welch 1982; Stutz and Sanderson 1983), diploids were significantly ($p < 0.05$) greater in plant height than tetraploids at all of the study areas and for both species (fig. 1, 2). Tetraploids and octoploids of Atriplex confertifolia were not consistently distinguishable, but the single decaploid population measured was larger in stature (fig. 2). Water potentials were less negative for diploids, even in Artemisia tridentata subspecies, where the two ploidy levels grew adjacent (South Table Mountain) or intermixed (Sage).

Soil electrical conductivity, a measure of salt concentration, was not significantly different for A. confertifolia ploidy levels at the sample size (one measurement per populations) (table 2). However soils for diploids ranged from 0.55 to 0.66×10^3 , while those for polyploids were above 1.00×10^3 (table 2) and follow trends similar to

Table 2--Soil characteristics for sampled *Atriplex confertifolia* sites

Ploidy	Location	E.C.x 10 ³	Percent sand	Percent clay	Percent silt	pH	Water table ¹
2x	Rush Valley	0.55	58	15	27	8.00	L
2x	Skull Valley	0.66	39	27	33	8.00	L
2x	Snake Valley	0.65	60	13	27	8.10	L
4x	Rush Valley	1.55	23	39	37	8.00	H
4x	Skull Valley	1.06	38	23	39	7.80	L
4x	Snake Valley	1.27	76	13	11	8.50	L
8x	Rush Valley	1.58	34	19	47	8.10	H
8x	Skull Valley	31.00	46	19	35	7.80	H
8x	Snake Valley	1.35	73	7	19	8.40	H
10x	Snake Valley	1.80	58	11	31	8.50	H

¹High or low water tables as shown by presence of the indicator species *Sarcobatus vermiculatus*.

those observed previously (Stutz and Sanderson 1983).

Electrical conductivity of leaf extracts (table 3) was significantly lower for tetraploids and significantly higher for decaploids. However, because a sizable proportion of the ions measured would be those sequestered in leaf hairs (Osmond and others 1980) which at undetermined times break and release their contents, uncertainty exists as to concentration within the other parts of the leaf. Another measure of osmotic capability might have been obtained from betain and other quaternary ammonium compounds. Our attempt to assay these compounds as the periodides proved difficult due to chemical instability (Storey and Wynn Jones 1977).

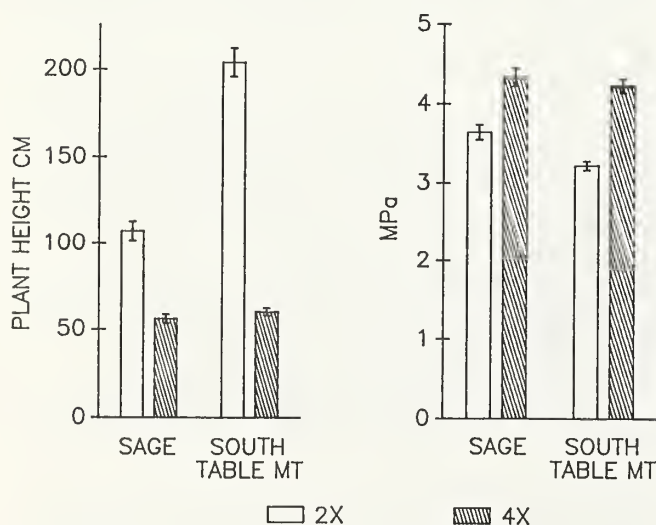


Figure 1--Plant height (left) and water potential (right) of *Artemisia tridentata* diploid (ssp. *tridentata*) and tetraploid (ssp. *wyomingensis*) plants at two sites in Wyoming, showing standard error.

DISCUSSION AND CONCLUSIONS

The cells of polyploids in comparison to those of diploids tend to be larger and their mitotic cycles slower (Stebbins 1950, 1971; Grant 1971), which often results in a larger macroscopic size of plant parts such as flowers and leaves, and sometimes of stature. However, at least in comparisons at the diploid and tetraploid levels, a stature relationship of this sort is not observed in natural populations of *Atriplex confertifolia* and *Artemisia tridentata*, nor in many woody species in which tetraploids are smaller than diploids (table 1). Further, Jones and others (1987) found that irrigated plants of *Artemisia tridentata* ssp. *wyomingensis* (tetraploid) in a common garden were much smaller and grew more slowly than those of ssp. *tridentata* (diploid). Because the cells of polyploids tend to grow more slowly, it is probably to be expected that shrubby polyploids should be smaller than diploids.

Reduced plant stature may be advantageous in relation to drought hardness. Jones and others (1987) found that unirrigated diploid *Artemisia tridentata* ssp. *tridentata* plants growing in an experimental planting had more negative water potentials than tetraploid ssp. *wyomingensis*, likely because of a greater demand by these large plants on soil moisture. Subspecies *tridentata* is notable in its restriction to microhabitats of greater moisture availability, such as the banks of washes or in valley bottoms. In its more common habitats, as shown by Barker and McKell (1983) and in both of our *Artemisia* study sites, diploid plants had less extreme water potentials in an arid season than adjacent tetraploids. Jacobsen and Welch (1987) have shown differential root growth patterns between ssp. *wyomingensis* and *tridentata* plants under greenhouse conditions. Probably the large diploids were able to tap a water supply not reached by ssp. *wyomingensis* roots (but see also Richards and Caldwell 1987). Given an equivalent water supply there might have been no differences, as was reported for the two subspecies growing on sand

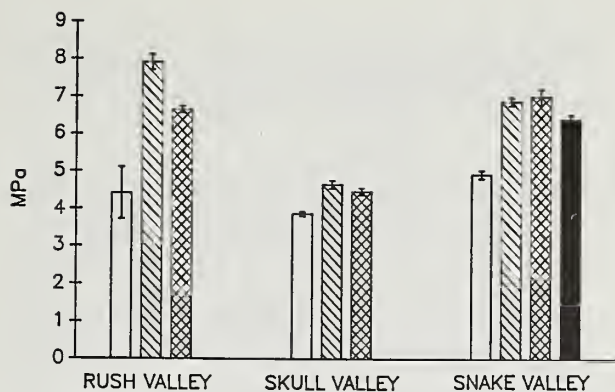


Table 3--Electrical conductivity of extracts of dried leaves of *Atriplex confertifolia* from Snake Valley, Millard County, UT. The ratio of dry weight to solution volume was 0.83 mg/ml

Ploidy	E.C. x 10 ⁻² mean	n	SNK test ¹
2x	29.9	10	A B
4x	26.8	10	B
8x	29.9	10	A B
10x	34.1	10	A

¹Means with the same letter are not significantly ($p < .05$) different.

dunes (Shumar and Anderson 1986). The smaller tetraploids would therefore probably fare better when on arid sites than diploids, which might tend to be eliminated.

As previously mentioned, diploids of *Artemisia confertifolia* likewise occupy more mesic sites than polyploids. Diploids of *A. confertifolia* at each of our three study areas occurred at higher altitudes than nearby polyploids and were the only populations occurring within arboreal vegetation zones (pinyon-juniper). Diploids were more robust, but not as dramatically so as the *Artemisia tridentata* diploids.

The presence of higher ploidy levels in *Atriplex confertifolia* allowed a continuation of measurements in that species up to the octoploid and decaploid levels. However, as previously discovered (Stutz and Sanderson 1983), instead of a continuation of the trend of decreasing stature, octoploids did not appear greatly different from tetraploids, and decaploids were taller than either (fig. 2). A possible reason for such a reversal of size relationships might be that there is an increased tolerance by polyploids of salinity (Tal and Giardi 1976; Tal 1980) as suggested by increased ionic content of leaf extracts at the highest ploidy (table 3, fig. 3). Polyploids of *A. confertifolia* often grow with *Sarcobatus vermiculatus*, an indicator of high (if saline) water tables (Kearney and others 1914; Meinzer 1937). This is particularly true of *A. confertifolia* decaploids. Water availability in such *Sarcobatus* areas, once a sufficient salt tolerance was present, might have allowed achievement of greater *A. confertifolia* statures.

The data collected here relate to stresses of arid climates and, in part, support Hagerup's Hypothesis. It seems probable for both *Artemisia tridentata* and *Atriplex confertifolia* that, through a reduced growth rate, tetraploids are more economical than diploids of moisture. In *A. confertifolia* in addition, there is a suggestion of greater salinity tolerance with increasing ploidy. Data from other physiologically stressful conditions, such as cold, may support Hagerup's Hypothesis as the Löves (1943, 1957)

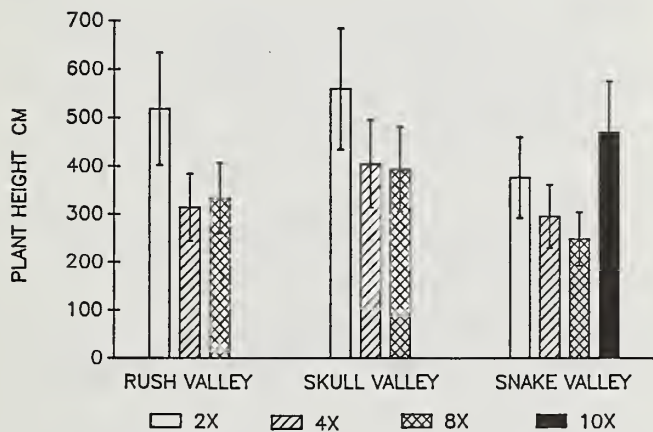


Figure 2--Water potential (above) and plant height (below) for diploids and polyploids and polyploids of *Atriplex confertifolia* at three areas in Western Utah, showing standard error.

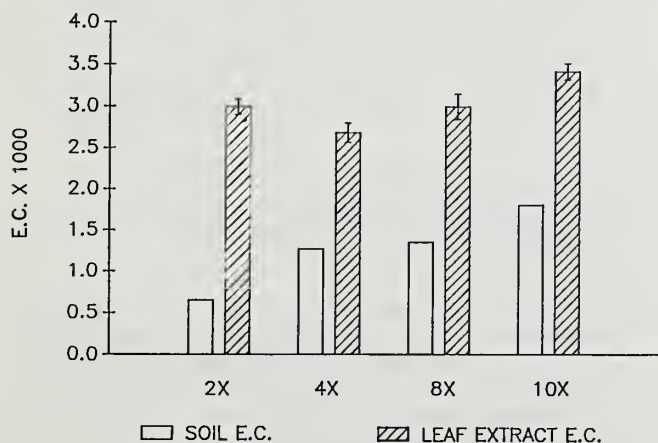


Figure 3--Relative soil and leaf extract electrical conductivity for four ploidy levels of *Atriplex confertifolia*, in Snake Valley. Leaf extracts were diluted to 0.83 mg dry weight/ml.

among others have suggested. We believe the intriguing question of ploidy/habitat relationships remains open.

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CELLULAR AND MOLECULAR APPROACHES TO THE ECOPHYSIOLOGY

AND GENETIC IMPROVEMENT OF SHRUBS //

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ABSTRACT: Financially immense private and national efforts are being made to apply cellular and molecular biology to agriculture. These efforts have resulted in revolutionary methodologies that could be used by the ecophysiologist/biochemist for understanding shrubs and shrub-environment interactions and ultimately by the shrub breeder/geneticist to genetically enhance germplasm. In this review consideration is given to selected methodologies and their current applications in plant research. Ecophysiological applications are suggested as well as some reasonable, not so futuristic, applications for shrub improvement.

INTRODUCTION

With little doubt biotechnology's premier expression in the plant sciences will be the identification, manipulation and successful transfer of agriculturally (or ecologically) important genes. Recent breakthroughs hold promise for development of cultivars that express greater yield capacity; that express greater resistance to insects as well as viral, fungal and bacterial infections; and that are resistant to environmentally safer broad-spectrum herbicides. Such research and its applications have been the subject of many recent reviews (Hess 1987, Cocking and Davey 1987, Potrykus and others 1987, Phillips and others 1987, Baulcombe 1987, Keen 1986, Goodman and others 1987) and will not be addressed here. Rather, this review focuses on several of the spinoff technologies of the molecular and cellular biologist; technologies that could be used by the plant scientist to better understand the interactions of shrubs with their environments and, eventually, to genetically enhance a shrub's ability to successfully cope with severe environmental stresses and perturbations. Subjects addressed in this paper include restriction fragment length polymorphisms, hybridoma technology, transposon tagging and studies involving mRNA.

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RESTRICTION FRAGMENT LENGTH POLYMORPHISMS

The purification of numerous enzymes that cut DNA at precise locations, based on a 4 to 7 base pair sequence (restriction enzymes), allows for the slicing of nuclear or plasmid DNA into fragments of specific lengths. Modern electrophoretic procedures permit separation of essentially homologous fragments that differ in length due to minor differences in base sequence at their restriction sites. Slight differences within or between organisms in the length of specific fragments can be detected by annealing labelled probes (RNA or cDNA), which are homologous to major portions of the fragments in question, to the electrophoretically separated DNA. Such polymorphisms in fragment length are referred to as restriction fragment length polymorphisms (RFLP's). RFLP's are codominantly inherited and, when represented in the plant in the heterozygous condition, can be mapped to other genetic loci by conventional methods (see Beckmann and Solter 1986). Linkage to previously mapped isozyme loci on tomato chromosomes has been accomplished for 120 different cDNA probes. The resultant linkage map now covers about 90% of the genome (Bernatzky and Tanksley 1986a, 1986b). Additional RFLP loci have been mapped to tomato chromosomes by Osborn and others (1987) and by Helentjaris and others (1986). The latter group also has greatly improved the chromosomal linkage maps of maize with the use of RFLP's.

Applications of RFLP's for evolutionary and genetic studies as well as for plant improvement are many. Until recently, quantification of polymorphisms for isozyme loci, as detected by differences in electrophoretic zymogram phenotypes, was considered the method of choice for determining extent of genetic variation within and between plant populations. Such variation has also been the subject of many taxonomic studies (see reviews in Tanksley and Orton 1983a and 1983b; Staub and others 1987). Today RFLP studies are rapidly replacing isozyme studies where such objectives are embraced. This is because the number of detectable RFLP's for a given taxon far exceeds the number of isozymes that could reasonably be used. Isozymes have other problems associated with them such as non-expression in certain tissues, possible differences between taxa in post-transcriptional modification, and questionable relevance in terms of natural selection. Restriction mapping and RFLP analyses of chloroplast DNA also provide meaningful information for systematic studies, especially

at the intergeneric and higher levels of taxa differentiation (Dutta 1986a, 1986b).

Isozyme and RFLP loci can be used in similar ways for plant improvement. First, such loci if found to be linked to important traits can be used to select individuals from backcross populations that contain alleles for the desired traits. This approach is of special value in introgressive hybridization programs where screening for the desirable introgression phenotypes is costly or overly difficult. Similar approaches also can reasonably be applied to quantitative traits. Nienhuis and others (1987) found that specific alleles linked to four RFLP loci accounted for 38% of the phenotypic variance for 2-tridecanone (a compound implicated in insect resistance in tomato) in a carefully selected population of F_2 's. Similarly, Osborn and others (1987) described linkage between RFLP loci and loci involved with soluble solids contents in tomato. These studies imply that potentially many RFLP loci can be correlated (or linked) with loci for quantitative traits such that accumulation of a select group of RFLP genotypes in a breeding program could result in individuals with maximal expression of the desired quantitative trait. Statistical procedures for such breeding schemes are already well developed (Stuber and others 1987; Nienhuis and others 1987; Edwards and others 1987; Beckmann and Soller 1986; Helentjaris and others 1985; Soller and Beckmann 1983). That restriction fragments homologous to sections of important genes can occasionally be isolated is evidenced by Vallejos and others (1986) who isolated fragments homologous with the rRNA (45s), the major chlorophyll A/B binding polypeptide and RuBP carboxylase genes.

It is evident from the above that there are several potential uses for RFLP's in shrub research. These include (1) high resolution in determining genetic variation and evolutionary divergence within and among taxa; (2) the rapid production of chromosome linkage maps, which should be most readily obtainable in outcrossing diploid species; and (3) use in breeding programs designed to introgress either simple or quantitative genetic traits among different genotypes.

HYBRIDOMA TECHNOLOGY

Hybridomas are monoclonal antibody-producing cells. They are generally produced by the fusion of an antibody-producing B-cell of an antigen-immunized animal with a myeloma cell, which renders the hybridoma potentially immortal. Many different hybridomas can be produced from an immunization with a specific antigen; the monoclonal antibodies of which may exhibit different properties, such as different levels of viral or enzyme inactivation (where the antigen was either a virus or an enzyme) or variable levels of specificity. Screening procedures are used to select, from members of a monoclonal library, monoclonals that exhibit desired properties. Such monoclonals can be labelled with an electron dense moiety for electron microscopy or with a radioactive moiety, biotin or a fluorochrome for light microscopy. Monoclonals so labelled can be used for the immunolocalization of antigenic surfaces in plant tissues or for quantification of specific biochemicals from plant extracts. A partial listing of plant-related antigens for which monoclonals have been raised appears in table 1. Procedures and other examples can be found in Gamble (1986).

Table 1--A partial listing of plant or plant-related substances for which monoclonal antibodies have been raised

Substance	Reference
Enzymes and proteins	
RuBP Carboxylase	(Vaughn 1987)
ferredoxin-nitrate reductase	(Ida 1987)
5-enolpyruvylshikimic acid 3-phosphate synthase	(Smart and Amrhein 1987)
phytochrome	(Schwarz and Schneider 1987; Silberman and others 1985)
wheat germ agglutinin	(Raikhel and Pratt 1987)
plasma membrane proteins	(Fitter and others 1987)
phloem lectin	(Smith and others 1987)
Plant growth regulators	
indoleacetic acid	(Mertens and others 1986)
gibberellic acids	(Knox and others 1987)
abscisic acid	(Raikhel and others 1986)
zeatin riboside	(Eberle and others 1986; Trione and others 1985, 1987)
Plant pathogens or parasites	
<u>Chlamydomonas eugametos</u>	(Homan and others 1987)
<u>Xanthomonas campestris</u>	(Yuen and others 1987; Leach and others 1987)
T-2 toxin of <u>Fusarium</u> spp.	(Gendloff and others 1987)
<u>Erwinia amylovora</u>	(Lin and others 1987)
wheat streak mosaic virus	(Sherwood 1987)
potato virus Y	(Rose and others 1987)
Others	
callose	(Grief and others 1987)

Labelled monoclonals for either microscopy or immunoassay generally provide results superior to those of other techniques. For example, Trione and others (1987), using a quantitative fluorescence enzyme immunoassay, quantified cytokinin levels as low as 0.03 pmol and Hainfeld (1987) electron microscopically visualized single antigen-binding antibody fragments by covalently linking an 11-atom gold cluster to such fragments. The number of plant-related antigens for which monoclonals have been produced is increasing as is the number of potential uses. Already, monoclonals for assaying plant growth regulators and some plant diseases are available commercially and study of plant-symbiont or plant-pathogen relationships using monoclonals or polyclonals (for the detection of additional molecular variants), including both infection sites and rates, is becoming commonplace. It is not unrealistic to suspect that monoclonals could be raised against the initial gene products that are produced by a shrub following an artificially imposed stress. Such monoclonals could then be used to study not only the initial gene products but also the sites and rates of stress response within and among genotypes.

TRANSPOSON TAGGING

Transposons (transposable elements) are DNA fragments that move in and out of chromosomes. In plants transposons range in length from about 0.4 to 8.3 kb (Doring and Starlinger 1986). Transposition of a transposable element into a gene (or its vicinity) generally causes a loss of gene function but on occasion can cause either an increase or decrease in gene function. Transposon-induced mutations frequently are unstable in that they can undergo germinal reversion, back to a wild type phenotype, at a rate as high as 2 to 3 percent. Such instability is a major diagnostic feature of transposons.

Recently, great interest has been placed upon the molecular isolation and cloning of transposons because once cloned they can be used to chemically isolate genes, for which knowledge of the gene product may or may not exist. Gene isolation by use of transposons (transposon tagging) involves the probing of restricted genomic DNA (from an organism in which a particular gene function has been altered by the insertion of a transposon) with labelled probes homologous to major portions of the transposon. By using a variety of restriction enzymes, it has been possible to extract and sequence entire genes from plant genomes (see Doring and Starlinger 1986 and Wienand 1986 for reviews). The cloning of genes tagged by transposons will likely be of immense value to the genetic engineering of plants. This is because one of the largest bottlenecks confronting the genetic engineering of plants is a lack of cloned agriculturally valuable genes.

It is believed that transposons are prevalent in plants (Nevers and others 1985; Vershinin and others 1987), particularly in natural populations of wild species where intense selection and breeding for uniformity has not occurred. Thus plant

scientists involved in the selection or utilization of shrubs may on occasion observe germplasm suggestive of unstable mutations. Such germplasm should be made available to interested geneticists and biochemists who can evaluate their potential for the isolation of additional transposons as well as for the tagging to genes that may be of agricultural or ecological importance.

STUDIES INVOLVING mRNA

In general plants respond to environmental stresses by either initiating and/or terminating synthesis of specific mRNA's. There are two approaches that can be taken to detect or quantify the mRNA's involved. First, if the biochemistry of the response is known, or plausibly construed, and if cDNA probes exist, then such probes can be used to quantify differences in the rate of synthesis of specific mRNA's. This is accomplished by isolating RNA from affected plant tissues at different times after exposure to the stress, purifying the RNA and dividing it into aliquots of varied concentrations, and either electrophoretically separating the RNA on gels or dotting specific aliquots to nitrocellulose and probing either the dotted or separated RNA with the labelled probes. For example, Esnault and others (1987) used the dot hybridization procedure and observed a major increase in mRNA's for phenylalanine ammonia-lyase and chalcone synthase within three hours after inoculation of a resistant soybean cultivar with zoospores of Phytophthora megasperma f. sp. glycinea. No increase was observed in the susceptible cultivar. These results were consistent with differences in synthesis of glyceollin, an antifungal compound, between the two cultivars following inoculation.

Changes in the presence or quantity of major mRNA's can be established even if the biochemistry of the stress response is not understood. This is accomplished by purification and *in vitro* translation of mRNA's, at various times following initiation of a stress, followed by electrophoretic separation of the polypeptide products. Using this procedure, Collinge and others (1987) detected differential major changes in gene expression when lettuce was inoculated with Xanthomonas campestris pathovars that were known to induce either a hypersensitive or a compatible response. Purification of the major polypeptides followed by substrate analyses could possibly lead to a better understanding of the biochemistry of such poorly understood responses.

Various mRNA analyses could enhance our understanding of the shrub-environment interaction. For instance much is known at both the physiological and biochemical levels concerning the response of plants to drought and water-logging, other soil component excesses, herbivory, and high and low temperatures. Analyses of gene expression in wild species immediately following initiation of such stresses would greatly extend our understanding of the biochemistry of resistance vs. susceptibility, tolerance vs. intolerance and responsiveness vs. nonresponsiveness among plant genotypes.

CONCLUSIONS

Evolution has resulted in a fantastic array of adaptations that function to moderate the biochemical effects of harsh environments. Many amazing examples occur within the environmental extremes of our terrestrial and aquatic worlds. The structural and physiological mechanisms of such adaptations have largely been described, yet little is known at the molecular level. It is at this molecular ecological interface, that recently developed biotechnological methodologies could make substantial contributions.

As physiological ecology enhanced ecological theory, so also will the advent of molecular ecology. Already monoclonal antibodies are being produced to study the biochemical stress response of plants to disease infestations. Such antibodies could be developed to probe a variety of ecological stresses. Plant infestation is also being studied at the level of differential mRNA synthesis and gene expression. Thus plant pathology is rapidly gaining a molecular basis. Such technologies coupled with others, such as the ability to precisely define plant genomes using RFLP's and to isolate genes by transposon tagging, promise plant biologists a menu of highly specific diagnostic, therapeutic and eventually even recreative scientific research.

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ORGANOGENESIS AND SHOOT-TIP MULTIPLICATION FROM TISSUE CULTURES OF ATRIPLEX SPECIES //

Jerry R. Barrow

ABSTRACT: Roots and shoots were successfully grown from callus cultures of Atriplex canescens and A. griffithsii in some experiments. Attempts to replicate organogenesis in callus or liquid cultures from these species and in A. acanthocarpa, A. confertifolia, and A. polycarpa were unsuccessful, indicating that specific genetic or cultural requirements were necessary for induction. Shoot-tips were multiplied rapidly after two months in culture from diploid (2x), tetraploid (4x), and hexaploid (6x), plants and from three different collections of 4x populations. Shoot-tip multiplication is a promising method of mass propagation of specific genotypes of Atriplex species.

INTRODUCTION

Atriplex species native to the more arid regions of western North America are a valuable component of rangeland for forage, cover, and revegetation of disturbed sites. They may potentially replace undesirable species or be used in marginal agricultural areas to provide forage with minimal or no irrigation. These native plants possess high genetic variability (McArthur and others 1983) and a remarkable ability to survive under extreme conditions. Therefore, they may be used as model systems to study stress tolerance and other survival mechanisms. If survival mechanisms can be identified and the corresponding genes isolated and transferred--using recombinant gene transfer technology--to other economically important plant species, then these other native plants would potentially be a resource of unique genes for stress tolerance and other useful traits.

Plant regeneration and *in vitro* propagation methods have been developed for a number of agriculturally important plants including agronomic plants, ornamentals, and trees (Conger 1980). By modifying methods, increasing numbers of plants are successfully being cultured. Norma Trolinda (personal communication) successfully regenerated plants from a collection of A. canescens, native to the Lubbock, Texas area, but was unsuccessful in regenerating plants from other A. canescens collections. Wochok and Sluis (1980)

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reported a method of shoot tip multiplication in A. canescens, with some spontaneous rooting. Apparently they were not successful in transferring rooted shoots to soil.

In the current research program, plant tissue culture methods were applied to Atriplex species to develop new approaches to shrub research. Cell cultures are used to study cellular responses to environmental stress and to develop unique selection methods. Plant regeneration capability would allow the recovery of valuable genes identified from *in vitro* experiments and allow their expression in whole plants. Shoot multiplication is a method of mass propagating specific genotypes for genetic studies, plant improvement, and other research approaches.

MATERIALS AND METHODS

In preliminary studies, embryos from two species, A. canescens and A. griffithsii, were removed from fruits and sterilized 7 min in 95% ETOH, then 20 min in 40% commercial bleach (2% sodium hypochlorite), and rinsed 30 min in sterile distilled water. They were germinated on 1/10 concentration EDS medium, which was modified from the B5 medium of Gamborg and others (1968), by Dunstan and Short (1977) with no growth regulators (table 1). Hypocotyls 1/2 to 1 cm long from A. griffithsii were plated on L2 medium of Phillips and Collins (1978) and labeled L2-C-init medium (table 2) to initiate callus. Callus was subcultured at approximately 1 cm in diameter, on the same initiation medium, and then subcultured monthly on L2-C-prlf to increase the quantity of the tissue. After 2 subcultures, the callus was transferred to L2-C-reg medium to induce regeneration. A similar sequence was used to culture A. canescens on the BDS series of media.

Callus cultures from five species, A. acanthocarpa, A. canescens, A. confertifolia, A. griffithsii, and A. polycarpa, were generated in the above manner and cultured on the L2 media series to determine their regeneration capacity. Liquid cultures were developed by culturing callus pieces in liquid L2-C-prlf medium on a rotary shaker under 16 h light, rotating at approximately 60 rpm.

Shoot-tip cultures were initiated from three cytotypes, diploid (2x), tetraploid (4x), and hexaploid (6x), plants described by Dunford (1984); and from 4x plants from three locations, one in west Texas, a high elevation site in New Mexico, and an arid site in southeastern Arizona.

Table 1--Nutrient concentrations of culture media

	Final concentration (mM)	
	BDS	L2
<u>Major salts</u>		
CaCl ₂	0.00	4.10
KNO ₃	23.20	20.77
KH ₂ PO ₄ ·H ₂ O	0.00	2.39
NH ₄ H ₂ PO ₄ ·H ₂ O	2.00	0.00
Na ₂ H ₂ PO ₄ ·H ₂ O	1.25	0.62
(NH ₄) ₂ SO ₄	1.01	0.00
MgSO ₄ ·7H ₂ O	1.00	1.76
NH ₄ NO ₃	4.00	12.50
FeSO ₄ ·7H ₂ O.EDTA	0.09	0.09

	Final concentration (μM)	
	BDS	L2
<u>Minor salts</u>		
H ₃ BO ₃	48.00	80.85
KI	2.20	6.02
MnSO ₄ ·H ₂ O	29.60	88.75
ZnSO ₄ ·7H ₂ O	3.50	17.40
CuSO ₄ ·5H ₂ O	0.08	0.40
Na ₂ MoO ₄ ·2H ₂ O	0.50	1.66
CoCl ₂ ·6H ₂ O	0.05	0.42

	Final concentration (mM)	
	BDS	L2
<u>Vitamins</u>		
Inositol	0.55	1.39
Thiamine.HCL	0.03	0.006
Pyridoxine.HCL	0.005	0.024
Nicotinic Acid	0.008	0.000

Other Additives

Sucrose	30.0 g per liter
Agar	6.0 g per liter
pH adjusted to	5.6

For multiplication, growing points approximately 1 to 2 mm were excised from the growing tip of germinating seedlings and cultured base down in BDS-G-Sm (table 2). Lateral shoots from mature plants were also collected, sterilized 20 minutes in 40% commercial bleach and rinsed in sterile distilled water. Then, 3 to 5 mm shoot-tips were excised and plated on BDS-G-Sm medium in 100 mm Petri dishes.

To induce rooting, individual shoots approximately 1 cm long, were excised from the shoot multiplication cultures and placed base down on the BDS-G-Rm medium and cultured in the growth chamber. All tissue cultures were incubated at 25 °C in a growth chamber with a 12 h light period.

RESULTS AND DISCUSSION

A total of 22 shoots developed from callus of A. canescens and 32 shoots from callus of A. griffithsii in the initial experiment, as a

Table 2--Growth regulator concentration of media

Media	Pic.(mg/l)	6,BA(mg/l)	GA	IAA
BDS-C-init	0.75	1.5	0	0
BDS-C-prlf	0.25	1.5	0	0
BDS-C-reg	0.00	0-4.0	0	0
BDS-G-Sm	0.00	0.5	4.0	0
BDS-G-Rm	0.00	0.0	0.1	0.5
L2-C-init	0.20	0.1	0	0
L2-C-prlf	0.10	1.5	0	0
L2-C-reg	0.025	1.0-2.0	0	0

response to decreasing picloram from 0.1 to 0.025 mg per liter and increasing 6, bensyladenine (6BA) to as high as 4.0 mg per liter in the regeneration medium. Because of the difficulty of maintaining A. canescens callus on BDS medium, all species were grown in L2 medium in subsequent experiments. Callus formed readily from both species and grew well in subcultures. Cell suspension cultures were readily initiated in liquid media from the callus cultures. Subsequent attempts to produce shoots on previously successful or modified media were not successful, indicating a genetic requirement or a specific nutritional requirement for organogenesis to occur.

Shoot multiplication experiments were generally successful independent of the cytotype or the collection used. This technique promises to be a useful method of replicating plants of a specific genotype. Tetraploid plants were the most responsive to shoot-tip multiplication, with several collections having shoots increasing 4 times every 10 days. This rate allows replicating large numbers of plants from a given selection quickly. Shoot cultures, at times, developed roots which were not specifically attached to shoots and they were not successfully transferred to soil. Specific rooting was initiated by excising single shoots from multiplication cultures and transferring them to a 1/2 strength rooting medium, BDS-G-Rm (table 2). After two weeks, roots began to develop at the base of the shoots. Rooted shoots were transplanted into peat pellets and covered with a beaker where they grew and were subsequently transplanted into soil where they were grown to maturity.

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RESPONSES OF CALLUS CULTURES, MICROSHOOT CULTURES, AND WHOLE PLANTS OF THE

HALOPHYTE, ATRIPLEX CANESCENS VAR. GIGANTEA TO EXOGENOUS NaCl

Eve Syrkin Wurtele

ABSTRACT: Plants, in vitro microshoots and calli of Atriplex canescens var. gigantea were continuously grown in media containing various levels of NaCl. Plants could grow in 1 M NaCl, however, microshoots and calli only grew on up to 100 and 300 M NaCl, respectively. The water and osmotic potentials of plants, microshoots, and calli decreased with exposure to decreased external water potential. However, the plants maintained water potentials significantly greater than the external water potential at all external NaCl concentrations. Microshoot water potentials were somewhat lower and calli water potentials were similar to the external media. In plants and calli, the turgor decreased with decreasing external water potential. However, the turgor of microshoots increased as the external water potential decreased. Cells of microshoots, but not plant or calli cells, responded to increased exogenous NaCl by expansion and increased trichome formation. In microshoots and calli, there was a correlation between the endogenous Na⁺ concentrations and survival, while plants survived with somewhat higher leaf internal Na⁺ concentrations. One explanation of this may be the apparent absence of functional trichomes on microshoots (or calli). Ion accumulation in cells of A. canescens was higher than that previously described for other cells, indicating a strong cellular basis for ion uptake. Mutagenesis of microshoots with ethylmethyl sulfonimide has resulted in a population of microshoots with increased salt tolerance. The mechanism(s) of this salt tolerance, and the salt tolerance of the corresponding plants, has yet to be determined.

INTRODUCTION

The genus Atriplex includes some very salt tolerant species, and biotypes from several of these species have great promise for utilization for biomass production, forage, and reclamation in arid and semiarid regions (Goodin and McKell 1971; McKell 1983), and as a source of triterpenoid saponins (Wurtele and others 1987). Within the genus Atriplex, a variety of mechanisms exist by which different species adapt to saline environments (Mozafar and Goodin 1970). Some mechanisms of salt tolerance operate at the cellular level, such as compartmentalization

of Na⁺ in the vacuole with a concomitant accumulation of nontoxic organic osmotic agents in the cytoplasm (Storey and others 1983) and increased succulence (Sharma 1982). Other mechanisms require higher levels of tissue organization, for example, compartmentation of salts in specialized cells such as trichomes (Mozafar and Goodin 1970), or substitution of K⁺ for Na⁺ at the root (Norton 1984).

By examining the ways in which whole plants, microshoots, and callus cultures respond to external NaCl we can gain a better understanding of the cellular and physiological mechanisms by which plants can maintain growth in highly saline environments. Such evaluations can also increase our ability to select various types of salt tolerance in vitro, and can facilitate the cloning of genes which play a critical role in salt tolerance.

Although the A. canescens var. gigantea (gigas) biotype is a prime candidate as a biomass species because of its rapid growth (Stutz and others 1975; McKell 1983), its salt tolerance has not been investigated. In this report we describe and compare the effects of external NaCl on the growth morphology, succulence, water relations, and K⁺ and Na⁺ content of callus cultures, microshoot cultures, and whole plants of A. canescens var. gigantea.

MATERIALS AND METHODS

Plants

Plants of Atriplex canescens var. gigantea (Welsh and Stutz 1984) = the gigas form of Stutz and others (1979) were originally obtained from cuttings from a single plant (genotype 9 female). Those plants were grown in the greenhouse as previously described (Wurtele and others 1987) and were utilized as the explant source for microshoot and callus cultures, and for obtaining cuttings as described below.

Cuttings (8 to 10 cm long) were obtained from these plants, and were rooted in tube containers (5 cm diameter, 25 cm length) which were filled with sand. After roots were established (3-4 weeks), the tubes were immersed in aqueous solutions containing Hoagland's macro- and micro-nutrients (Hoagland and Arnon 1950) with varying concentrations of NaCl. The solutions were changed at monthly intervals.

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Microshoot Culture

Apical buds and axillary buds were used as the explant source of shoot multiplication, by a modification of a previously described method (Wurtele and others 1987). Sterilized lateral bud explants were aseptically placed in a culture tube containing Murashige and Skoog salts and vitamins (Murashige and Skoog 1962), 3% sucrose, and 0.6% Difco agar (basal medium), supplemented with 1 mg l⁻¹ benzyladenine (BA). The shoots were grown in a daily cycle of 16 h of fluorescent light in cycles of 27 ± 2°C 8 h of dark at 25 ± 2°C.

Shoot clumps were subcultured at monthly intervals. For each subculture, the tops were removed from shoots which were over 2 cm in height. Shoot clumps were then divided into pieces each consisting of three or four shoots, attached at their base. These pieces were transferred to fresh medium and grown under the conditions described above.

Three or more months after initiation, microshoots were placed in basal medium with 1 mg l⁻¹ BA and added NaCl. These microshoots were grown and subcultured at monthly intervals as described above.

Callus Culture

Leaves that were almost fully expanded were washed in tap water for 2 h, surface sterilized for 10 min in 1% NaOCl, and rinsed three times in sterile distilled water, and utilized as the explant source for callus cultures. Explants were placed abaxial side down onto the basal culture medium supplemented with 0.5 mg l⁻¹ 2,4-dichlorophenoxyacetic acid (2,4-D). Two months after initiation, calli were divided into pieces of 0.4 to 0.6 g fresh weight and subcultured onto fresh medium. Calli were grown under cycles of 16 h of fluorescent lights at 27 ± 2°C, and 8 h of dark at 25 ± 2°C.

Growth Measurements

Fresh weights were determined for plant material from 10 replicate jars, each jar containing three explants right after subculture. Half of the explants were dried in a drying oven for 48 h and individual dry weight determinations were obtained. The remaining half were allowed to remain on the medium under the growth conditions described previously. After 30 days, fresh and dry weight determinations were made for the remaining explants. All experiments were repeated at least once.

Water Relations

Water potentials of plants were measured with a Scholander-type pressure chamber (PMS Instrument Co., Corvallis, OR). Shoots were collected at 10 a.m. and pressure-volume curves were generated (Scholander and others 1965; Tyree and Hammel 1972) from which the osmotic potential and turgor were calculated.

At the time of subculture, the water potentials of the microshoot and callus cultures were measured with C-30-Sf sample chambers connected to an HP-115 Microprocessor Controlled Water Potential Data System (Wescor, Inc.; Logan, UT) in the dew point (hydrometric) mode. Osmotic potentials of calli and microshoots were measured by the same method after the same tissue was frozen in liquid nitrogen and then thawed. Turgor was calculated as the difference between the water and osmotic potential. All experiments were repeated at least once.

Analysis of Na⁺ and K⁺

Endogenous concentrations of Na⁺ and K⁺ were determined by atomic absorption spectrophotometry of oven-dried plant parts (0.1 to 0.25 g dry weight), digested with concentrated nitric acid (Haulin and Soltanpour 1980).

Scanning Electron Microscopy

Scanning electron microscopy (SEM) was performed on plant material growing in 0, 100, 150, or 500 mM NaCl media. Plant material was fixed in 1% aqueous osmium tetroxide, and then coated with additional osmium tetroxide by the OTO method of Kelly and others (1973). The specimens were dehydrated in a graded ethanol series and dried from CO₂ by the critical point method (Anderson 1951). Samples were sputter-coated with gold, and examined at 10 KeV or at 15 KeV in a Hitachi S-450 SEM. Several samples of each type of plant material were observed and the micrographs represent typical samples.

Selection of Material for Analysis

All material analyzed was from plants or cultures grown for 4 to 6 months (with subcultures) on medium containing a specific concentration of added NaCl. Leaves which were almost fully expanded were utilized for all studies of plant leaves.

RESULTS AND DISCUSSION

Growth

The growth rates of plants, microshoots, and calli grown in the different concentrations of added NaCl were determined.

The shoots of plants grown in all levels of NaCl increased in height (table 1). The growth rate was maximal between 0 to 100 mM NaCl and was lowest at 1 M NaCl. Plants grown in all concentrations of NaCl appeared morphologically similar. In contrast, though, the microshoots grew vigorously on media containing no added NaCl and even more vigorously on 50 mM NaCl, growth on medium containing 100 mM NaCl, expressed as an increase in fresh weight, was very low (table 1). The microshoots which were subcultured on 300 mM

Table 1--The increase in growth of *A. canescens* var. *gigantea* grown in media containing additions of NaCl

	NaCl(mM)	% increase/30 days
Shoots of whole plants ¹	0	154
	100	145
	500	133
	750	131
	1000	109
Microshoots ²	0	1100
	50	960
	100	260
	300	(dead)
Callus Cells ²	0	496
	50	607
	150	432
	300	169
	500	(dead)

¹Increase in height, results are means of three replicates.

²Increase in weight, results are means of five replicates.

NaCl for 3 months did not survive (data not shown). Microshoots grown without added NaCl were dark green and appeared healthy. Those grown on 50 mM NaCl were lighter green and the leaves showed increased succulence. The microshoots grown on 100 mM NaCl were light green and vitreous, with very succulent leaves.

Callus growth occurred on media containing up to 300 mM NaCl (table 1). The relative growth rate, based on fresh and dry weight, was greatest for calli growing on 50 mM NaCl. The relative growth rate of calli was similar on 0 and 150 mM NaCl. Growth was considerably reduced for callus exposed to 300 mM NaCl. Calli grown on 0 and 50 mM NaCl were bright green; calli grown on 150 mM NaCl were either green or greenish-white; calli grown on 300 mM NaCl were whitish-brown. The majority of cells grown on 0 to 150 mM NaCl were small spherical cells (30 to 50 μ m diameter).

Correlations between the level of salt tolerance of callus cultures and in whole plants have been found for several species (Tal and others 1978; Orton 1980; Smith and McComb 1981), including the halophytes, *Suaeda martima* (Von Hedenstrom and Breckle 1974), *Spartina spicata* (Warren and others 1985), and *Distichlis spicata* (Daines and Gould 1985). However, no such correlation has been found for *Suaeda australis* (Smith and McComb 1981), *Salicornia herbacea* (Stroganov 1973), or *A. undulata* (Smith and McComb 1981).

For both microshoots and calli of *A. canescens*, growth was greater at 50 mM than at 0 mM NaCl (growth in 50 mM NaCl was not examined for whole plants, although the growth of plants of several species of *Atriplex* is stimulated at 50 mM NaCl [Jeschke and Stelter 1983]). Thus, a small amount of NaCl added to the media actually stimulates

growth both *in vivo* and *in vitro*. Such a growth increase at 50 mM NaCl was not found for calli of *A. undulata* (Smith and McComb 1981) growing in a similar medium and in a similar environment.

Water Relations in Response to Exogenous NaCl

The water potential of shoots from *A. canescens* var. *gigantea* plants grown in 750 mM NaCl was over threefold lower than in 0 mM NaCl; osmotic potential was twofold lower at 750 mM NaCl than at 0 mM NaCl (fig. 1). This is similar to the water and osmotic potentials of shoots from

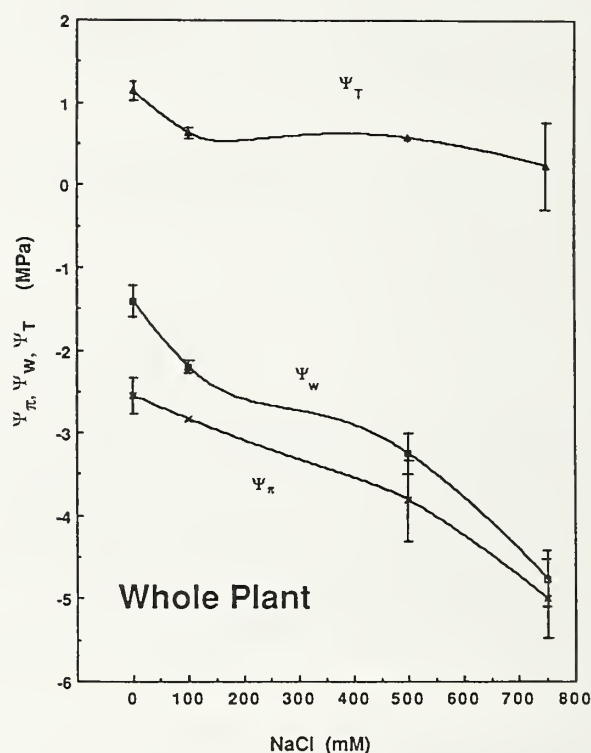


Figure 1--Water potential, osmotic potential, and turgor of plants grown in solutions containing different concentrations of NaCl.

plants of several *Atriplex* spp. which decrease as plants are grown in soils of decreasing water potential to (e.g. Storey and Jones 1979; Osmond and others 1980; Sharma 1982; Gale and others 1970; Riehl and Ungar 1983). In microshoots and calli of *A. canescens*, growth in higher levels of NaCl similarly resulted in decreased water and osmotic potentials (figs. 2, 3), indicating a cellular basis for these responses.

The osmotic potential of the shoots of plants was in all cases lower than that of the microshoots which was lower than that of the callus cells at any given exogenous concentration of NaCl (figs. 1-3). This could be caused by morphological and anatomical differences (such as the presence of

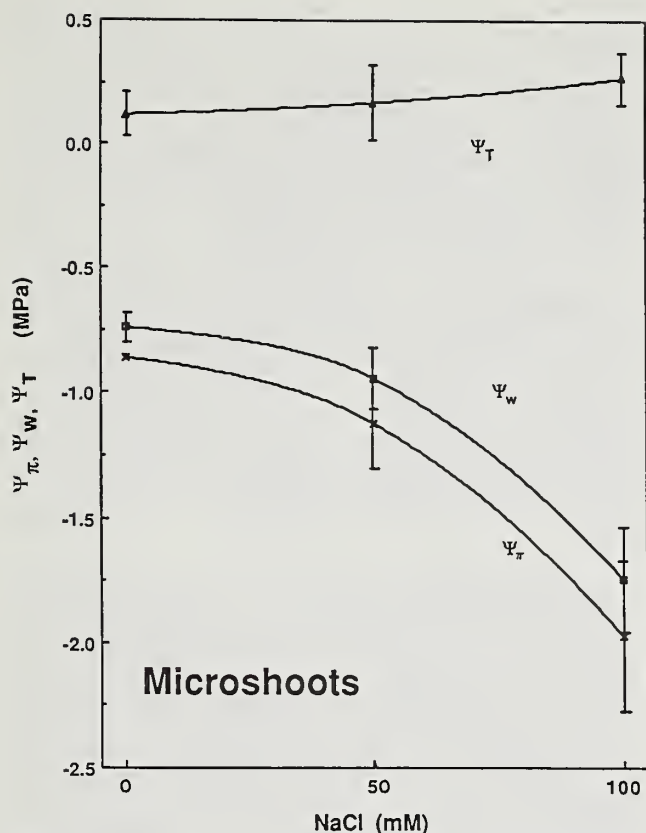


Figure 2--Water potential, osmotic potential, and turgor of microshoots grown on media containing different concentrations of NaCl.

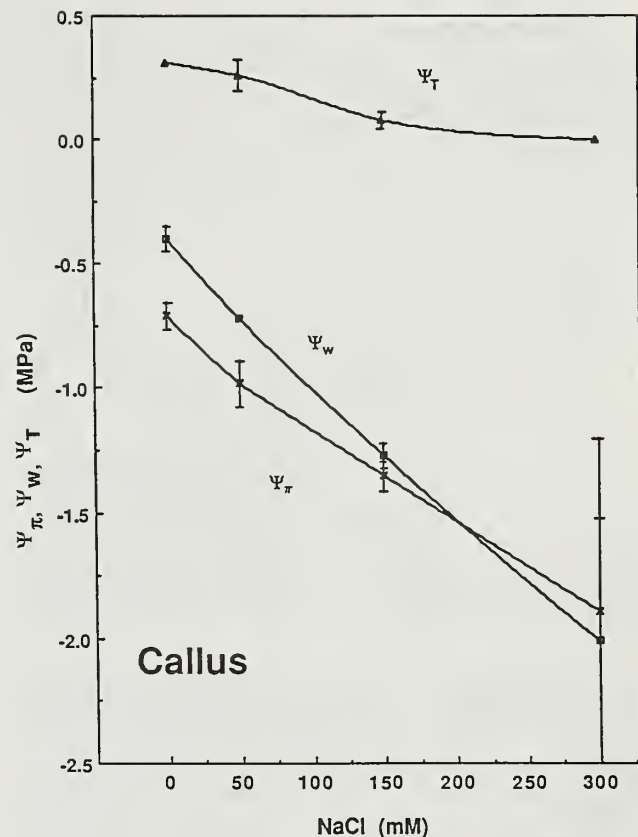


Figure 3--Water potential, osmotic potential, and turgor of callus cells grown on media containing different concentrations of NaCl.

roots or trichomes) which promote greater uptake and accumulation of salt and/or synthesis of organic osmotic agents by the intact plant. Additionally, the lack of differentiated vascular elements in callus tissue probably further restricted uptake of water and salts into callus tissue. The lower osmotic potential of the shoots of plants compared to the microshoots and calli could also have been, in part, a consequence of differences in the ambient environment. The decreased humidity in which the plants were grown could further add to a greater flow of water and dissolved salts into the intact plant.

The shoot turgor decreased for *A. canescens* plants grown in increasing NaCl, e.g. at 0 mM NaCl the turgor was almost fivefold higher than at 750 mM NaCl. In calli, turgor also decreased with increasing NaCl, from 0.31 MPa at 0 mM NaCl to 0 MPa at 300 mM NaCl. Our results for the turgor of salt-adapted *A. canescens* var. *gigantea* callus cells are similar to those which can be calculated from osmotic potential determinations for salt-adapted suspension cells of the halophyte *Distichlis spicata* (Daines and Gould 1985). Interestingly, this decrease of turgor in cells of these two halophytes grown in high NaCl contrasts to an increase of turgor reported for water-stressed suspension cells of the glycophyte, tobacco (Handa and others 1983).

Unlike the behavior of the shoots of plants and the callus cells, the osmotic potential of the

microshoots over-compensated in response to increased NaCl in the media, such that the turgor actually increased with increased salinity of the growth medium. To our knowledge, no other studies have been made of the effect of NaCl on microshoot turgor. Such studies in glycophytes and in other halophytes might help to elucidate the mechanisms of turgor maintenance and osmotic compensation.

Na⁺ and K⁺ Content

The accumulation of high levels of Na⁺ in leaves is a characteristic of successful halophytes growing in high Na⁺ (Flowers and others 1977; Osmond and others 1980). The concentrations of Na⁺ and K⁺ were determined for leaves and roots of plants, leaves of microshoots, and callus of *A. canescens* var. *gigantea* grown in various concentrations of NaCl. The K⁺ content on a dry weight basis was fairly constant in leaves of plants grown in solutions containing a wide range of added NaCl (fig. 4). In contrast, Na⁺ concentrations increased sharply in plants grown in solutions with higher levels of exogenous NaCl. The Na⁺ concentration in leaves was about 16-fold higher in plants grown in 500 mM NaCl medium than in plants grown in medium without added NaCl (fig. 5). Up to 12% of the dry weight of *A. canescens* var. *gigantea* leaves was due to Na⁺; this is about 10 times greater than the Na⁺ content reported for a polyploid *A. canescens* by

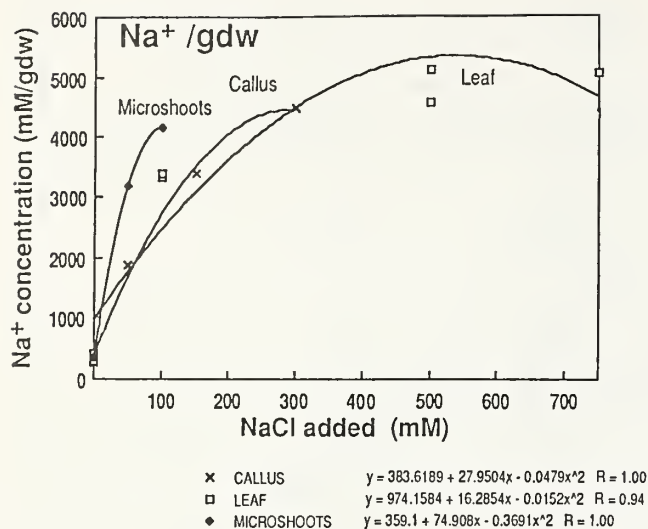


Figure 4--Potassium content of shoots of plants, microshoots, and callus cells grown with different concentrations of NaCl.

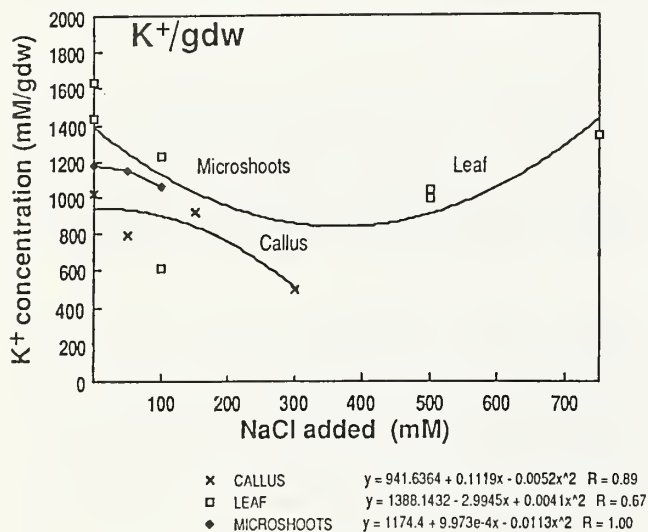


Figure 5--Water potential, osmotic potential and turgor of callus cells grown on media containing different concentrations of NaCl.

Wallace and others (1982). As for several other *Atriplex* genotypes (Mozafar and others 1970; Sharma 1982; Wallace and others 1982; Storey and others 1983), the K⁺ content of the *A. canescens* var. *gigantea* plants did not change significantly over a wide range of exogenous Na⁺ concentrations.

The Na⁺/K⁺ ratios reported for leaves of different *Atriplex* genotypes grown at a given concentration of NaCl vary widely (e.g. Chatterton and others 1970; Storey and Jones 1979; Osmond and others 1980; Ruess and Wali 1980; Wallace and others 1982). The Na⁺/K⁺ ratios for *A. canescens* var. *gigantea*, which ranged from 0.1 for leaves of plants grown in 0 mM NaCl solution to 2 or 3 for leaves of plants grown in higher NaCl concentrations, are similar to those of two

biotypes of tetraploid, hydroponically grown *A. canescens* (Norton and others 1984). However, the Na⁺/K⁺ ratio for a field grown polyploid *A. canescens* genotype indigenous to a particularly harsh environment (Ruess and Wali 1980) was over 10 times greater than that for *A. canescens* var. *gigantea*. Thus, although accumulation of Na⁺ is high in *A. canescens* var. *gigantea*, it may be higher still in other *A. canescens* genotypes, i.e. those with greater salt tolerance.

For *A. canescens* var. *gigantea*, the Na⁺/K⁺ ratio is similar for calli, microshoots, and leaves of plants grown in the same concentration of NaCl. This similarity of Na⁺/K⁺ ratios may indicate that the relative uptake of the Na⁺ and K⁺ ions has a broad cellular basis, and is not solely dependent on the presence of roots or of a specific root cell type. These Na⁺/K⁺ ratios cannot account for the relatively much greater NaCl tolerance of the *A. canescens* var. *gigantea* plants.

A correlation between the level of salt tolerance in the whole plant and in the callus has been demonstrated for several species (including both glycophytes and halophytes), and the absence of such a correlation has been demonstrated for others (e.g. Dix and Street 1975; Tal 1978; Smith and McComb 1981). Callus cells of *A. canescens* var. *gigantea* showed little salt tolerance compared to that of the whole plants. This is similar to what was reported for *A. canescens* var. *gigantea* (Smith and McComb 1981), although recent observations indicate that callus cultures of at least two other *Atriplex* genotypes may have much higher NaCl tolerance (J. Goodin and J. R. Barrow, personal communication).

The relationship between the salt tolerance and ion uptake for plants and calli has only been examined in a few cases. The Na⁺ and/or K⁺ concentrations in NaCl adapted cells of the glycophytes *Nicotiana tabacum* and *Citrus cinensis* (Heyser and Nabors 1981; Ben-Hayyim and Kochba 1983; Lerner and others 1985), the moderately salt tolerant *Medicago sativa* (Croughan and others 1978), and the ahlophyte *Distichlis spicata* (Daines and Gould 1985) have been analyzed previously. The Na⁺/K⁺ for the *A. canescens* var. *gigantea* callus cells adapted to a given concentration of NaCl is less than half that of the comparable salt-adapted cells of tobacco. The absolute level of Na⁺ in *A. canescens* var. *gigantea* cells is about two-to eightfold higher than in tobacco, citrus, alfalfa or *D. spicata* cells, and the concentration of K⁺ in the *Atriplex* cells is two- to tenfold higher than in tobacco, citrus, or alfalfa cells. Thus, the ionic uptake responses of the halophyte *A. canescens* appear to be quite different from those of tobacco, alfalfa, or *D. spicata*, indicating a species dependent cellular basis for ion uptake, with much higher levels of ion accumulation occurring in *A. canescens*. Furthermore, these data are consistent with the notion that the *Atriplex* cells are able to tolerate higher levels of internal Na⁺ than can cells of tobacco. Perhaps *A. canescens* var. *gigantea* cells have more efficient mechanisms for subcellular compartmentalization of ions in the vacuole.

Morphology and Succulence

One response associated with growth in high NaCl is increased succulence. For the diploid *A. canescens* var. *gigantea*, we found only a 12% to 18% increase in plant leaf succulence. Leaves of plants in 100 to 750 mM NaCl solutions could not be readily distinguished by visual and SEM observations from leaves of plants grown in 0 mM NaCl (fig. 6). There was little or no increase in the diameters of mesophyll or epidermal cells in leaves of NaCl grown *A. canescens* var. *gigantea* plants, although such increases have been reported for *A. patula* (Longstreth and Nobel 1979). Trichome size appeared to be only slightly greater for leaves of NaCl-grown *A. canescens* var. *gigantea* than for leaves of plants grown in medium with added NaCl. Therefore, an increase in leaf succulence does not appear to be a major mechanism for NaCl tolerance in the whole plant of *A. canescens* var. *gigantea*.

In contrast, the ratio of fresh weight to dry weight of *A. canescens* var. *gigantea* NaCl grown microshoots was about twice that of the microshoots grown without added NaCl. Furthermore, leaves of microshoots grown on 100 mM NaCl medium were visibly thicker and larger than their counterparts grown on 0 mM NaCl medium, and displayed a marked increase in the diameter of mesophyll and epidermal cells, but not bundle sheath cells (figs. 7, 8). Increased succulence has been attributed to high Cl levels (Flowers and others 1977); it is possible that Cl uptake differs between plants and microshoots of *A. canescens* var. *gigantea*.

Atriplex which use the C3 and C4 photosynthetic pathways have been reported (Osmond and others 1980). Leaves of one biotype of tetraploid *A. canescens* (Norton and others 1984) appear to have "Kranz anatomy." The leaf cross sections of *A. canescens* var. *gigantea* displayed typical "Kranz anatomy" (fig. 8), indicating that this diploid variety is likely also C4.

Few studies have compared the internal leaf anatomy of plants to that of *in vitro* microshoots, and this is, to our knowledge, the first such study of a C4 plant. Wetzstein and Sommers (1982) demonstrated a marked decrease in the degree of organization of the mesophyll tissues of the microshoot leaf compared to those of the plant leaf for sweet gum. Our examination of *Atriplex* microshoots indicates a similar decrease in mesophyll organization. Furthermore, the bundle/sheath strands are less developed, and difficult to distinguish from the mesophyll cells. In addition, the mesophyll and epidermal cells of the microshoot leaf are very vacuolate, in sharp contrast to the cytoplasmically dense cells of the plant leaf.

Another difference between leaves of plants and those of microshoots is the presence of a more highly developed cuticle on the plant leaves (Wetzstein and Sommers 1982). It has been hypothesized that the trichomes of *A. halimus* plants growing in salt do not absorb water despite a large increase in salt content because they are surrounded with a cuticle which is

impermeable to water (Mozafar and Goodin 1970). Although we do not have data on cuticle thickness for *A. canescens* var. *gigantea*, our observations are consistent with these reports. The trichomes of *A. canescens* var. *gigantea* microshoots growing on medium containing added NaCl are greatly expanded in comparison to those of microshoots growing on medium without added NaCl, whereas the trichomes of the corresponding plants are only slightly greater in size.

The number of the microshoot trichomes was much lower than for leaves of plants grown on 0 mM NaCl solution. Also, microshoots grown on 0 mM NaCl medium had a much lower trichome density than microshoots grown on 100 mM NaCl medium. Thus, environment, as well as genetics (Osmond and others 1980), appears to have a great effect on trichome density and morphology.

The callus cells showed a 15% to 20% increase in succulence in response to exogenous NaCl. However, the cell size was similar (fig. 9) with a slightly greater proportion of large cells in the 0 mM NaCl calli.

Interestingly, the callus of *A. canescens* var. *gigantea* is somewhat more NaCl-tolerant than is the more organized microshoot. Although the microshoots have trichomes, it is not clear that they function. Cytoplasmic density of the stalk cells has been correlated with functioning trichomes (Kelley and others 1982), and the stalk cells of the microshoot leaf are much less cytoplasmically dense than those of the plant leaf. Perhaps, factors such as high humidity, absence of a cuticle, and/or altered photosynthesis impair trichome function in the microshoot. A toxic concentration of Na⁺ could, therefore, accumulate in the cytoplasm of the cells of the microshoot causing the low tolerance of the microshoots to external NaCl. Clearly, the increase in leaf succulence observed for the microshoots exposed to NaCl is not sufficient to confer high salt tolerance. The slight increase in succulence of the callus together with a somewhat lower absolute concentration of Na⁺ and K⁺ might explain the somewhat greater salt tolerance of the callus compared to that of the microshoot.

Selection of Callus Cells and Microshoots With Increased NaCl Tolerance

Callus cells and microshoots were grown for prolonged period (12-14 mo) in 300 and 100 mM external NaCl, respectively. In no case did an increase in salt tolerance occur, as evidenced by a similar monthly growth rate over a 12-month period. This is somewhat surprising in view of the fact that even cells of many glycophytes such as tobacco (e.g. Dix and Street 1975) develop an increased tolerance to external NaCl. Microshoots also did not increase in NaCl tolerance even after 13 months of selection on NaCl-containing medium.

Microshoots were treated with the mutating agent ethylmethyl sulfonimide (EMS) and allowed to multiply. After a period of 13 months, only



Figure 6--SEM of leaves of plants of *A. canescens* var. *gigantea*. A,B) plants grown without added NaCl; C,D) plants grown with 100 mM added NaCl; A,C) adaxial; B,D) abaxial. Surface views at identical magnifications.

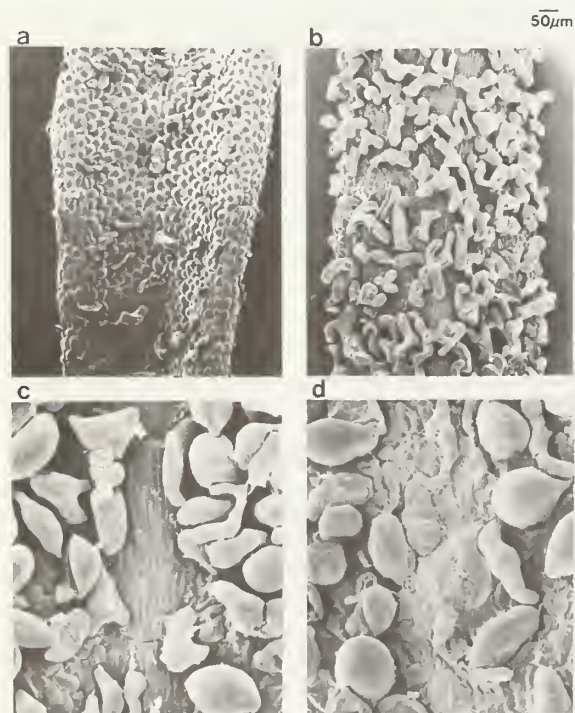


Figure 7--SEM of leaves of microshoots of *A. canescens* var. *gigantea*. A,B) microshoots without added NaCl; C,D), microshoots grown with 100 mM added NaCl; A,C, adaxial; B,D), abaxial. Surface view at identical magnifications.

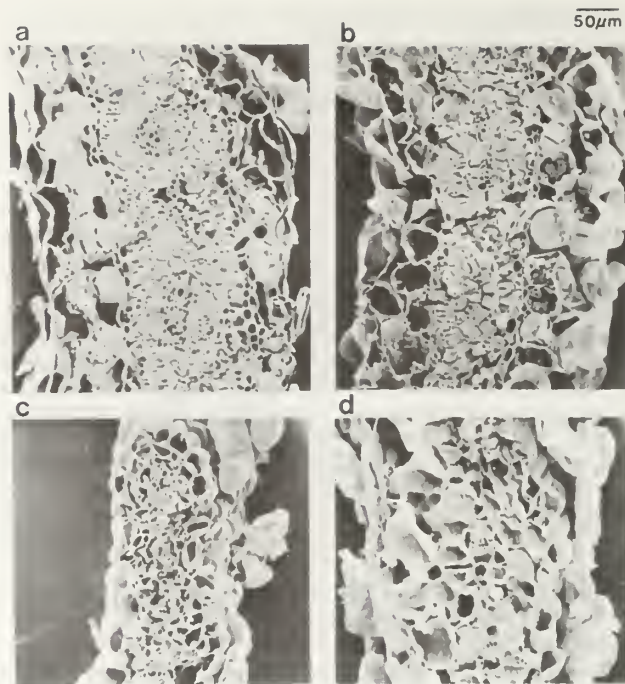


Figure 8--SEM of callus cells of *A. canescens* var. *gigantea*. A,B) callus cells grown with added NaCl; C,D) callus cells grown with 100 mM added NaCl. Surface views at identical magnifications.

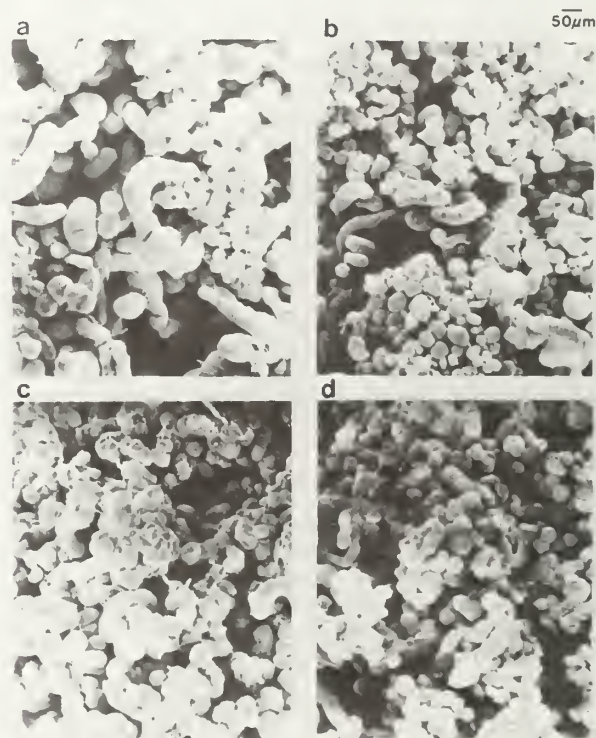


Figure 9--SEM of leaves of plants (a,b); and leaves of microshoots (c,d) of *A. canescens* var. *gigantea*. A,C) grown without added NaCl; B,D) grown with 100 mM NaCl. Cross sectional views at identical magnifications.

Table 2--Multiplication rates for shoots of A. canescens var. gigantea (genotype 9 female) pretreated with EMS and transferred onto media containing 0, 100, and 300 mM NaCl. Cultures were divided and transferred at monthly intervals

		Transfer			
EMS	NaCl	1	2	3	13
% mM		Multiplication Rate			
0	0	3.8 ± 1.7	3.3 ± 1.7	3.4 ± 1.9	3.3 ± 1.0
1	0	3.2 ± 1.3	4.3 ± 1.4	2.5 ± 0.8	3.6 ± 1.1
2.5	0	2.8 ± 1.2	3.6 ± 1.5	3.0 ± 0.9	4.1 ± 2.4
0	100	1.2 ± 0.8	2.2 ± 1.0	0.8 ± 0.3	----
1	100	N.D.	1.3 ± 0.6	0	----
2.5	100	N.D.	1.7 ± 1.1	1.9 ± 0.8	1.4 ± 0.7
0	300	N.D.	0	0	----
1	300	N.D.	0.8 ± 0.3	0	----
2.5	300	N.D.	0.5 ± 0.2	0	----

Table 3--Responses of Atriplex canescens var. gigantea to growth in increased external NaCl

	Shoots of Whole Plants	Microshoots	Callus Cells
Growth	Survive to > 1 M NaCl	Survive to 100 mM NaCl	Survive to 300 mM NaCl
(Na+) internal	Always higher than (Na+) external		
(K+) internal	Always higher than (K+) external		
Cell size	Similar	Large increase	Slight decrease
Succulence	Slight increase	Large increase	Moderate increase
Ψ w internal	Higher than Ψ w external	Slightly higher than Ψ w external	Similar to Ψ w external
Ψ w internal	Approaches Ψ w internal	Decreases faster than Ψ w internal	Approaches Ψ w internal
Turgor	Decreases to 0	Increases	Decreases to 0

microshoots derived from treatments with 2.5% EMS were surviving in 100 mM NaCl (table 2). These microshoots are now being rooted and the resultant plants will be tested for NaCl tolerance. The mechanism of the increased NaCl tolerance is not clear, however, salt tolerant and the nonsalt tolerant microshoots could lead to the identification of genes involved in physiological responses to salt tolerance.

CONCLUSION

The responses of A. canescens var. gigantea plants, microshoots, and calli to various levels of external NaCl are summarized in table 3. A cellular basis for salt tolerance, as reflected in an ability of cultured cells to grow on high salt medium, is not evident for A. canescens var. gigantea. However, the ability to accumulate high levels of ions at all levels of tissue organization appears to be a characteristic with a strong cellular basis in this taxon. The study of in vivo and in vitro responses to NaCl provides potential for 1) gaining a greater understanding of salt tolerance, 2) the development of in vitro systems to increase salt tolerance, and 3) the isolation of genes involved in salt tolerance.

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Section 2—Environmental Management and Technology

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TRANSPANTING OF NATIVE SHRUBS ON DISTURBED

LAND IN THE MOJAVE DESERT

E. M. Romney, A. Wallace and R. B. Hunter

ABSTRACT: Restoration of native shrubs on disturbed land is a very slow natural process in the Mojave desert; however, the time required can be shortened markedly with managed transplanting and husbandry procedures. Tests conducted on denuded desert land in southern Nevada have shown that native shrubs can be transplanted at reasonable cost to obtain significant cover and density within a 5 to 7-year period by using selected species, by protecting them from grazing jackrabbits, and by supplying nutrient supplements.

INTRODUCTION

Findings presented are from experience gained from shrub transplanting work at the Nevada Test Site on land denuded by blading and grading. Study sites are located in shrub-dominated ecosystems in the Mojave desert and in the transition zone between the Mojave and Great Basin deserts. Shrub transplanting work is an ongoing program supported by the U.S. Department of Energy, Nevada Operations Office, to restore shrub vegetation onto land disturbed by energy development activities. From this program we have learned several things about what must be done to insure survival and growth of transplanted native shrubs within reasonable cost. Emphasis, therefore, will be placed upon procedural findings rather than upon data from specific experiments.

TRANSPANTING METHODS AND MAINTENANCE

During earlier phases of this work, considerable effort was devoted to developing cost-effective methods for producing native shrub transplant specimens. This involved propagation from rooted cuttings and from seed germination (Wieland and others 1971). The goal was to learn how to restore a mixed population of native shrubs back to near-pristine state on denuded desert land. We found that this is possible; however, it is not economical due to the high cost of propagation and the slow growth and development of most

native shrub species. In order to economically restore shrub vegetation onto large disturbed sites, it is more efficient to transplant only those species which are easy to propagate and which have hearty survival, growth and development characteristics. Mojave desert shrubs most suitable for transplanting are Atriplex canescens, A. polycarpa, A. lentiformis and Larrea tridentata. Ambrosia dumosa also does well in the Mojave Desert, but not in the transition zone between Mojave and Great Basin deserts. Great Basin desert species include Artemisia tridentata, Ceratoides lanata, Chrysothamnus nauseosus and Lycium andersonii. In cases where a broader mix of shrub is preferred for landscaping purposes, the costs for propagation and maintenance, plus time for growth and shaping, are principal limiting factors (Romney and others 1979, 1980, 1981).

Young Seedling Preparation and Planting

We found two procedural methods to be effective for large-scale shrub transplanting. One is to obtain 9 to 12-month old seedlings from commercial sources grown in 10-15 cm long tube-pack containers with arrangements for delivery to the job site for transplanting when it becomes frost-free in early spring. The best transplanting period for sites involved in this study is March through April, after which time supplemental irrigation is not usually required unless the preceding winter season precipitation was below normal. In most cases the top meter of soil on sites denuded for longer than a year will have adequate stored moisture to insure transplanted seedling survival, growth and development when spaced at densities of around 1000 plants per hectare. Commercial seedlings specimens normally are prepared with fertilizer supplement in sufficient amounts to carry the plants during the first season after transplanting. When it becomes necessary to transplant shrubs on sites with low soil moisture, we set out the seedlings with 2-3 liters of water and form a berm around each specimen to accommodate supplemental irrigation. Applications of 4-5 liters of water at 6-week intervals normally will satisfy needs through hot, dry summer months until fall season stress-dormancy occurs. The objective is not to promote succulent growth but rather to minimize the development of new foliage until succulent tissues harden over winter and the plants break dormancy with rapid growth and development the following spring. We rarely lose more than

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Figure 1--Shrub specimens potted in plastic tubes and grown under glasshouse conditions in preparation for transplanting.

ten percent of transplanted specimens using the procedure described when adequate grazing protection from jackrabbits is provided.

Older Seedling Preparation and Planting

The second procedural method that has proved to be efficient is to propagate plant material on a continuing basis, and develop two or three-year old transplant specimens from excess commercial seedling stock, from seedlings germinated from locally collected seed, and from rooted cuttings. Seedling specimens are potted into 7.5 cm dia. flexible, black plastic tubes provided with slow bottom drainage. Tubes 35 cm long are filled to 30 cm with a one-to-one mixture of soil and vermiculite. A slow release, urea-based complete fertilizer pellet is placed near the bottom of each tube to provide a source of essential nutrients to the potted seedling. The potted shrub specimens are stored erect in plastic-lined holding boxes and developed under glasshouse conditions with minimum irrigation until transplanted (fig. 1). This procedure provides an ongoing stock of hardened shrub specimens to meet transplanting needs that are difficult to plan for and schedule. Such specimens can be transplanted any time between March and September irrespective of low surface soil moisture because of their deeper root configuration and greater moisture holding capacity. Upon transplanting, the lower half of the plastic tube is slipped up around the upper half when the shrub specimen is planted in a hole dug by hand or by power auger. Water (4-5 liters) is added to set the soil around the specimen and a berm is formed to accommodate later irrigation when required. The double ply of plastic around the upper half of the transplanted root system serves as an important barrier preventing moisture loss to the surrounding surface soil (fig. 2). Again, the first year objective is to avoid rapid growth of succulent foliage. For this reason supplemental water is applied only during the period between transplanting and onset of seasonal dormancy.



Figure 2--When transplanted, part of the potting tube is wrapped up around the root system to help reduce water loss to dry surface soil.

Grazing Protection for Transplanted Specimens

An important lesson learned is the necessity of providing each species of transplanted native shrub with adequate protection from grazing jackrabbits and livestock. One must decide, therefore, which kind of protective fencing is to be employed at given transplanting sites. Livestock grazing has been prevented since the early 1950's in areas of the Nevada Test Site of interest to our work, so we have only had to provide protection from jackrabbits. Depending upon the size of the job site and its future use, one may have an option of erecting a rabbit-proof perimeter fence around the transplanted area or of placing an individual fence around each shrub specimen. The cost for each method of fencing is about the same but each has certain advantages. Greater biomass can be obtained with perimeter fencing that prevents grazing, but the integrity of the fence must be maintained. In areas where perimeter fencing is not permitted, individual protective fences can be erected of size to prevent no grazing or to permit some grazing (compare fig. 3 and 4). Inasmuch as light grazing and pruning generally enhance growth and development of shrubs, we generally elect to protect each specimen with a dome-shaped cover made of 5 cm. dia. wire mesh netting that will keep jackrabbits from destroying the root crown but allow them to graze on shoots that protrude beyond the wire cover. The covers are made from 90 cm-wide poultry netting cut into 60 cm segments. The wire mesh is folded and the cut wire segments twisted together along each edge.

The open bottom of the formed cover is spread apart and placed over the transplanted shrub specimen. Soil pushed up around the cover to form an irrigation berm will lock the wire mesh in place (fig. 5). These covers do not need to be removed since shrub branches can grow out freely through the wire mesh openings. We have found that 90 cm-wide, 5 cm-dia. wire mesh attached to 120 cm-long steel fence posts at 3 meter spacing will provide rabbit-proof perimeter fencing. Wire



Figure 3--Seven-year-old transplanted shrubs protected with individual wire netting. Note loss of basal biomass to grazing jackrabbits.



Figure 4-- Seven-year-old transplanted shrubs growing within rabbit-proof fenced enclosure. Note increased basal biomass when protected from grazing jackrabbits.



Figure 5--Transplanted shrub specimen with wire netting cover and shallow berm for adding water if needed.

need not be tacked to the ground between posts when erected on level land since the jackrabbit will not burrow underneath. Other burrowing small animals, except gophers, cause insignificant grazing damage. The problem with gophers will be discussed later.

RESULTS AND DISCUSSION

Several ecophysiological relationships influence the success of shrub transplanting on disturbed, denuded land and some will be addressed herein. If a broader treatise is desired, readers are referred to a series of papers in Great Basin Naturalist Memoirs, Number 4 (Wallace and others 1980).

Selection of Shrub Species

In order to economically restore shrubs onto disturbed Mojave desert land by managed transplanting methods, one must be satisfied to use only a few species that are easy to propagate and that survive and grow well under the harsh environmental conditions. We have listed above those species which are the most easy to propagate, hearty to survive and which undergo rapid growth and development after transplanting. Sufficient time has not passed at any of our study sites to experience natural input of slower growing species, but our planting density of around 1000 plants per hectare provides plenty of room between plants for other shrub species to become established. New progeny seedlings have appeared around transplanted host shrubs within five years, but they generally do not survive unless they are protected from grazing animals. By using those shrub species listed with the transplanting and fencing methods described above, the cost for producing transplant specimens and placing them onto disturbed sites with protection from grazing jackrabbits ranges from 3 to 5 dollars per specimen.

An additional problem worth mentioning is competition that occurs for soil moisture from the summer annual Salsola species that commonly invade disturbed land areas at the Nevada Test Site (fig. 6). Those annual plants are fierce competitors because of their unique germination, survival, and growth characteristics (Rhoades and others 1967; Wallace and others 1968). They should be removed from around the transplanted shrubs to reduce competition for available water.

Animal Grazing Problem

It was mentioned above that all livestock grazing has been curtailed at our study sites, but it should be a problem at sites requiring shrub revegetation elsewhere on open rangeland. It is imperative that transplanted shrubs be adequately protected from grazing jackrabbits (Lepus californicus) and gophers (Thomomys bottae) in order to insure survival. While the effect from gophers might not be immediate, as is the case with jackrabbits, the long-term effect is disastrous. For example, 162 transplanted specimens consisting of 14 different shrub species planted in 1972 were



Figure 6--Illustration of competition problem between the transplanted shrub located at center of photo and surrounding summer annual Salsola population.

reduced to 110 in 1973, 60 in 1977, 50 in 1978, 22 in 1983 and 7 in 1986 in an area infested by pocket gophers. It is not economical to transplant shrubs into gopher infested areas unless chemical eradication measures have been taken. Even then there may be long-term losses as revegetated sites become reinfested.

In several instances we have lost virtually overnight almost all transplanted shrubs set out without fencing to protect them from grazing jackrabbits. One must realize that an average 5-6 kg animal requires up to 200 gm of succulent plant foliage daily in order to obtain sufficient water for survival. Their target material grazed for food and water is principally new shrub seedlings; therefore, aside from drought, jackrabbits are simply the single most limiting factor governing natural restoration of shrubs in the Mojave desert. We have demonstrated at bladed and graded sites that shrub recovery can be enhanced markedly by protecting new seedlings, new crown sprouts, and resprouts from sheared-off root systems with wire mesh covers at the start of the spring growing season after disturbance has occurred (Hunter and others 1985). Problems resulting from transplanting shrubs later during the summer season become intensified because jackrabbits will seek out the succulent plant material for water and consume all unprotected, aboveground tissue.

Nutritional Supplements

Blading and grading Mojave desert land not only destroys long-standing vegetation, but it also destroys the delicate fertile islands formed underneath shrubs over long periods of time (Romney and others 1980). A major problem in shrub restoration is to restore that nutrient

resource to the disturbed area. We have tried several methods to do this, including the addition of chemical fertilizers by dry broadcast and also wet applications onto the surface, by addition of nutrients to irrigation water, and by the addition of steer manure and sewage sludge amendment both onto the surface and mixed into pocket zones. Surprisingly, the best and most cost-effective method proved to be the one described of placing slow-release, complete fertilizer pellets in the potting tube while preparing shrub seedling specimens for later transplanting. This does not imply that the other methods are ineffective; they can be effective when the fertilizer supplements are applied sparingly. The situation is that, since native shrubs are relatively slow growing, they do not require very high levels of soil fertility. In fact, the addition of fertilizer in amounts and by methods normally applied to agricultural crop plants will often inhibit shrub growth unless accompanied by supplemental irrigation or rainfall. We believe that this results from the addition of more salt to soils already high in soluble minerals.

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PULSE ESTABLISHMENT OF WOODY SHRUBS ON DENUDED MOJAVE DESERT LAND //

E. M. Romney, A. Wallace and R. B. Hunter

ABSTRACT: Denuded Mojave desert land usually requires decades of time for restoration of woody shrubs through natural revegetation processes. We had opportunity to observe pulse establishment of Ambrosia dumosa and Larrea tridentata onto land that had been disturbed by grading followed by rare events of above-normal rainfall in southern Nevada. Grazing jackrabbits severely damaged unprotected new shrubs. Findings on survival and development of cohort seedling populations indicate that this pulse-triggered establishment of new shrubs resulted from two successive years of above-normal summer rainfall, plus normal winter precipitation, following the year of germination.

INTRODUCTION

Woody shrubs in Mojave desert ecosystems are long-lived, and their turnover in established populations is correspondingly slow (Shreve and Hinckley 1937; Johnson and others 1975; Beatley 1976, 1980; Hunter and others 1980; Vasek 1980). There are, however, distinct age classes in shrub populations, indicating that periodic pulse establishment normally occurs (El-Ghony and others 1980; Romney and others 1980). Storm-initiated germination followed by high seedling mortality is typical of those ecosystems (Went and Westergaard 1953; Sheps 1973; Ackerman 1979).

Mojave desert land denuded by various kinds of disturbance usually requires decades of time before woody shrubs regain even a semblance of original cover and density (Vasek and others 1975; Romney and others 1980; Wallace and others 1980; Webb and Wilshire 1980). Land at the Nevada Test Site in southern Nevada has been denuded at various locations by different kinds of energy development activities. We present herein some observations and data on pulse-triggered establishment of woody shrub seedlings on northern Mojave desert land denuded by grading.

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EXPERIMENTAL SETTING AND METHODS

An area in Jackass Flats was denuded by grading to a depth of 15-20 cm in April, 1979, after which it was occupied as a military bivouac area for six weeks until abandoned. The area was then made available for conducting revegetation experiments within a Mojave desert shrub community dominated by Larrea tridentata and Ambrosia dumosa. The alluvial soil of the area is sandy to depths greater than one meter. Our interest at this particular site was an opportunity to investigate regrowth of woody shrubs from new sprouts on sheared-off root systems.

Periodically we have encountered examples of shrub rejuvenation from new sprouts on exposed and sheared-off root systems. This has been observed mainly with Larrea tridentata, Lycium andersonii, and Ephedra nevadensis, but it probably occurs with other shrub species as well. The question arose concerning the extent to which one might speed up natural revegetation by protecting new sprouts on sheared-off root systems from grazing animals.

The recently graded site provided an opportunity to investigate this process and develop cost-effective procedures to compare with transplanting methods that have proved to be successful. We learned from earlier shrub transplanting experience that the transplanted specimens need protection from grazing rabbits in order to assure their survival. That problem arose not from normal pruning of shoots, which is beneficial in promoting new growth, but from excessive pruning of palatable shoots down to (and often including) the root crown. Jackrabbits have shown preference for grazing on transplanted shrub specimens even when succulent native vegetation is standing nearby; we presume that a sense of taste is involved.

After summer rainfall in May and July, 1979, new sprouts grew on exposed roots and denuded crowns of Ambrosia dumosa and Larrea tridentata. Specimens located within a one-hectare area were measured for size and covered with wire mesh screens for protection against overgrazing by jackrabbits. Survival and growth of this population was monitored periodically until December 1983.

Concurrently with the root and crown sprout experiment, we transplanted some specimens of Atriplex canescens and Larrea tridentata onto the graded site with and without protective screen covers. Virtually all of the unprotected transplants had been destroyed by December, 1980, and none survived until October 1981. Jackrabbits

also had grazed on foliage of Larrea that extended beyond the screen covers, and the animals had kept the foliage of Atriplex clipped back to the screen wire which we observed each time we visited the study site through December 1983. Again, we presume that a sense of taste might be involved since we produce the transplant specimens in glasshouse under high nutritional conditions.

Two cohort populations of randomly spaced Ambrosia dumosa seedlings that germinated in the graded area following summer rainfall in 1981 were marked in April 1982 to follow survival and development. Another cohort population of A. dumosa seedlings was identified in one square meter quadrats along 50-meter belt transects in both the graded and adjacent undisturbed areas after pulse-triggered germination of new seedlings following above-normal rainfall in August 1983. What followed was an unusual pulse of survival and development of new shrubs in the graded area concurrent with subsequent years of above-normal summer rainfall, plus normal winter precipitation.

RESULTS AND DISCUSSION

Table 1 contains data on survival and growth of shrubs from resprouts on sheared-off root systems that had been covered with protective screens. Specimens marked and left unprotected did not survive overgrazing by jackrabbits and stress from late summer and fall drought in 1980. We observed that some jackrabbit grazing on new sprouts had occurred at the time the study population was marked, and we continued to find evidence that jackrabbits grazed from foliage that had grown outside of the protective screen covers when we made periodic visits to the graded study site through the remainder of 1979, 1980, and 1981.

Table 1--Survival and growth of Ambrosia dumosa and Larrea tridentata shrubs from resprouts on sheared-off root systems protected by wire screens

Observation Time	Surviving population	Mean size cm ³ ± S.E.
(x 10 ³)		
<u>Ambrosia dumosa</u>		
August 1979 ¹	34	0.25 ± 0.7
August 1980 ¹	29	22.4 ± 2.8
December 1980 ²	24	4.4 ± 1.0
October 1981 ¹	23	26.7 ± 3.8
December 1983	18	241 ± 30
<u>Larrea tridentata</u>		
August 1979 ¹	27	2.7 ± 0.8
August 1980 ¹	17	15.0 ± 4.0
December 1980 ²	16	32.0 ± 6.0
October 1981 ¹	15	131 ± 26
December 1983	15	836 ± 162

¹Lightly grazed by jackrabbits. ²Heavily grazed.

Very heavy grazing occurred during the late fall drought period of 1980, especially on Ambrosia dumosa, but the screen covers prevented destruction of the new sprouting crowns. Loss of some new sprout specimens occurred for other reasons than overgrazing, presumably from severe moisture stress. However, during the five-year observation period, at least one half of the original new sproutings had become well established shrubs of vigorous size (table 1 and figures 1 and 2). Our findings suggest that the practice of placing screen wire covers over succulent resprouts on sheared-off shrub root systems to protect them from overgrazing by jackrabbits is an inexpensive way to help speed up the restoration of shrubs onto disturbed and denuded Mojave desert land.

The first opportunity to observe pulse-triggered establishment of shrub seedlings on the graded area in Jackass Flats resulted from thunderstorm systems that impacted that site during summer months of 1981. Table 2 gives precipitation data measured at a location 11 km from the graded site



Figure 1--View of the graded area in Jackass Flat taken August 1982. The larger shrubs are resprouts from sheared-off root systems protected from overgrazing by jackrabbits after August 1979.



Figure 2--View of the graded area taken in October 1985 after pulse establishment of new shrubs following successive years of above-normal summer and normal winter precipitation in 1983 and 1984.

Table 2--Precipitation (mm) at U.S. Weather Bureau Station located 11 km NE of graded study site at comparable elevation

Month	1978	1979	1980	1981	1982	1983	1984	1985
January	58.2	27.9	38.3	06.6	05.3	31.2	00.0	12.7
February	73.9	13.2	25.6	00.2	06.1	09.1	03.8	03.1
March	76.2	34.8	44.9	41.6	42.6	76.2	00.0	02.8
April	13.4	00.2	02.5	00.2	07.1	08.1	00.3	00.0
May	00.1	10.4	10.4	18.0	07.8	12.2	00.0	25.6
June	00.0	00.0	01.7	00.0	00.0	00.0	00.0	00.8
July	02.5	13.9	05.1	20.3	01.5	00.0	114.3	09.4
August	01.0	08.9	00.0	05.1	11.4	98.8	44.2	00.0
September	22.8	00.0	05.8	08.4	10.1	06.8	07.6	17.1
October	17.5	00.0	00.0	00.0	00.5	02.0	03.8	01.5
November	19.0	00.2	00.0	08.9	16.7	13.9	25.2	27.4
December	10.1	08.9	00.0	00.0	06.3	21.6	61.7	04.3
Total	294.7	118.4	134.3	109.3	115.4	279.9	260.6	104.7

Table 3--Survival and growth of *Ambrosia dumosa* seedlings on graded site in west Jackass Flats

Time and Group Survival		Mean Size		¹ Growth Constant
	n	cm ³ \pm S.E.	(x10 ³)	k
<hr/>				
<u>April 1982</u>				
Group 1	31	6.9	\pm 1.1	
Group 2	31	7.9	\pm 1.3	
<u>November 1982</u>				
Group 1	30	30	\pm 7	2.9*
Group 2	29	22	\pm 4	2.0
<u>December 1983</u>				
Group 1	27	189	\pm 25	1.9
Group 2	29	153	\pm 20	2.1

¹Growth constant, $k = [\text{size } 1 / \text{size } 2] \text{ t}$; in years.

*significantly different at $p = .05$ by signed rank test.

at comparable elevation. Table 3 gives data on survival and growth of two cohort groups of *Ambrosia dumosa* seedlings that was attributable to successive years of above-normal summer and winter precipitation following germination.

A large pulse of new shrub seedling germination also was triggered again during the years of 1983 and 1984, but the establishment pattern was extremely different between the graded area and the surrounding natural vegetation area (table 4). Within three years after pulse germination, cover and density of new *A. dumosa* shrubs in the graded area exceeded that of adult shrubs in the surrounding undisturbed area (Hunter 1987). Figures 1 and 2 are views illustrating new shrub seedling establishment on the graded area over a 3-year period. Pulse-triggered germination of new shrub seedlings in the undisturbed area was as high as 170 per m², but proportionally few survived from environmental stress factors, including grazing jackrabbits. As many as 20 seedlings per

Table 4--Survival of pulse germination of *Ambrosia dumosa* seedlings in m² quadrats along 50-meter belt transects across a graded and undisturbed site in west Jackass Flats. Seedlings were counted on January 11 and August 17, 1984, and on September 11, 1987

¹ Quadrat	Bladed Site			¹ Quadrat	Undisturbed Site		
	Jan. 84	Aug. 84	Sep. 87		Jan. 84	Aug. 84	Sep. 87
1	48	22	20	1	151	5	1
2	23	11	8	2	204	3	0
3	25	4	5	3	318	26	6
4	17	5	6	4	438	11	3
5	43	16	11	5	124	9	1
6	71	21	13	6	418	23	6
7	28	5	6	7	864	4	0
8	40	13	13	8	115	3	0
9	14	9	8	9	805	9	0
10	97	20	19	10	195	28	3
Total	406	126	109	Total	3,632	121	20

¹Grouped in sets of 5 m² for convenience of listing in table.

m² were counted on the graded area of which a greater proportion survived and made a marked impact as viewed in figure 2. Because of the combination of stresses from competition with adult shrubs for water and from animal grazing, relatively few new seedlings survived in the surrounding undisturbed area as compared to the higher number of seedlings that survived on the graded site. We also found that the proportion of seedlings of different shrubs and grass was unexpected. For example, on one transect of 1 m x 150 m there were 5,527 A. dumosa seedlings, 15 Larrea tridentata seedlings, 3 Acamptopappus shockleyi seedlings and 43 Oryzopsis hymenoides seedlings (Hunter 1987).

Competition for water among new shrub seedlings was completely different in the graded and the adjacent, undisturbed area. The cohort of new shrub seedlings in the undisturbed area was surrounded by old adult shrubs in competition for available water. Therefore, relatively few seedlings survived beyond the first year after germination and grew to 5-cm size in any dimension within the observation period. In the graded area there was no competition for water between new seedlings and adult shrubs, except around the border where the suppressed size of established seedlings was evident within 5 to 7 meters from undisturbed, adult shrubs. Farther out into the graded area the surviving seedlings did not compete with one another, so they continued vigorous growth and development. Inasmuch as water did not become limiting in the graded area, the result was a phenomenal display of new shrub growth and development during the successive years of above-normal precipitation in 1983 and 1984. Competition between young plants for longer term survival is an interest that we shall continue to follow with this new shrub population.

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HIGH-TECH POLYACRYLAMIDES AS SOIL CONDITIONERS IN THE RECLAMATION

AND STABILITY OF DESERT LANDS //

Garn A. Wallace and Arthur Wallace

ABSTRACT: Water-soluble polyacrylamide polymers with appropriate characteristics serve several useful purposes in land reclamation projects. They are especially economically affordable when applied in irrigation water, although they may also be applied to soil as dry granules. When applied to tilled soil, soil aggregates are made more water stable with resulting increases in pore space in soil. Less surface crusting, improved water penetration and drainage, more resistance to erosion, less capillary rise of salty water are among the effects which follow. Although these soil conditioners replace the need for addition of large quantities of organic materials to the soil in the reclamation process of desert lands, best effects are achieved when the polymers and a modest amount of organics are applied together. When soils are saline and sodic, the use of the polymers results in making soil more permeable so that salts are more easily leached, and applied gypsum is more effective in replacing sodium on the clay in the soil. Waste management involving arid lands can be improved in combination with use of the new polymers.

INTRODUCTION

Although super absorbent water-insoluble polymers have uses in soil preparation (Azzam 1985; Henderson and Hensley 1986), they are not the subject of this paper. The polymers that swell on addition of water to sometimes several hundred times their volume are cross-linked to achieve that property. These cross-linked polymers can be useful, especially in sandy soils low in water-holding capacity. They are available to the home and landscape trades.

In 1952 Soil Science (Bear 1952) published a set of papers that introduced synthetic polymer soil

conditioners to the scientific community. Monsanto Chemical Company released a product known commercially as Krilium. Enthusiasm was high during the early 1950s because of the urgent need for improving the physical properties of soils; however, the realization that the methodology was too expensive for use became apparent after a few years. It was also too expensive for specialty uses, although other problems resulted in its total withdrawal from the market in the early 1960s.

Worldwide interest has continued in this area until the present time. Several reviews and symposia have monitored progress in the field. Azzam (1980) reviewed the subject including over 500 references. In our own work we had used the Monsanto product of Krilium all during the 1960s and 1970s, having obtained a large supply when it was still available. Azzam's review caused us to examine a number of new polymer chemicals as soil conditioners, some of which were already in our laboratory for other reasons, and we also prepared some in our laboratory.

Emerging from the pieces of work is the hope of a new technology that can easily and economically remove the most important remaining barrier or limiting factor to soil improvement. This barrier is poor physical properties of soil, which limits water movement, root development, and aeration of the soil.

As the world gears up for new major advancements to result from biotechnology and genetic engineering, soil scientists must concern themselves with the creation of soil conditions that would permit full expression or full potential of the new developments. New high technology soil conditioners can help make this possible.

With new soil conditioner materials and new methods of application, the amount of soil conditioner needed to improve a given area of land can approach two orders of magnitude less than that used 35 years ago (Wallace and Nelson 1986).

The new water-soluble soil conditioners may, if used according to established procedures

1. Increase pore space in soils containing clay.
2. Increase water infiltration into soils containing clay.
3. Prevent soil crusting.
4. Stop erosion and water runoff.
5. Make friable soil that is easy to cultivate.
6. Make soil dry quicker after rain or irrigation so that the soil can be worked sooner.

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Consequently, these translate into

1. Stronger and larger plants with more extensive root systems.
2. Earlier seed emergence and crop maturity.
3. More efficient water utilization.
4. Easier weed removal.
5. More response to fertilizers and amendments.
6. Less plant disease related to poor soil aeration.
7. Decreased energy requirements for tillage.

These developments will also make it possible to better achieve land reclamation, especially in difficult situations (Ferguson and Frischknecht 1983).

CONTROL OF SOIL EROSION BY POLYMERIC SOIL CONDITIONERS

Soil losses resulting from action of rain have been a tremendous problem to man since his beginning (Black and Adams 1984; Crosson and Stout 1984; Wallace and Wallace 1986). The impact of a rain-drop on unprotected soil tends to break down soil structure, and surface flow transports the detached soil. Air escaping from aggregates immersed in water causes them to explode if they are unstable (Kemper and others 1985). The slaking that results can lead to either sheet or gully erosion. If water reaches the same aggregates very slowly, however, they may not explode. A well-known control of erosion by water is the establishment of a vegetative cover where possible. Grasses are commonly established to serve this purpose as they cushion the fall of raindrops and minimize the slaking or detachment of soil particles. With surface soil stabilized in this manner, infiltration is increased, and runoff and erosion are reduced.

Because grass is usually established by seeding, erosion must be temporarily controlled until the grass is adequately developed. Vegetative mulches, usually consisting of straw, hay, or grass, are generally applied over newly seeded sloping surfaces. Disadvantages of mulches include flammability, bulk, unsightliness, high-application costs, and, in many instances, unavailability of mulch (Weeks and Colter 1952).

The resistance of soils to erosion is related to the components of soil organic matter that produce stable structure in soil. A friable crumb structure that is resistant to slaking by water is less likely to result in soil movement during rain or irrigation. The essence of arable soil is the presence of sufficient stable organic compounds capable of binding clay particles into water-stable aggregates. Not all organic materials are capable of forming water-stable aggregates, however. Decaying organic matter releases some substances that are capable of aggregating soil (Oades 1984). Bacterial slimes and fungal mycelia are important means of soil aggregation.

In an experiment, simulated rainfall (12.7 mm in 2 min) was applied to 11.4 by 11.4-cm containers. The polyacrylamide was applied simulating an aerial application (crop dusting airplane) for the dry applications. The soil was on a 15° slope.

The results indicate that the rate 16.8 kg ha⁻¹ of the polyacrylamide applied to the soil surface as a dry powder fully stopped erosion under the conditions tested (table 1). The lower rates were also highly successful. The polymer applied in solution was fully effective in stopping erosion.

Table 1--Effect of dry-broadcasting a polyacrylamide on damp soil for erosion control

Treatment	Rate of polyacrylamide kg ha ⁻¹	Erosion MG ha ⁻¹	Reduction %
Sandy clay (crusting soil) from Lancaster, Calif.			
Control	0.0	5.10	-
Level 1	5.6	0.57	89.7
Level 2	11.2	0.14	97.3
Level 3	16.8	0.00	100.0
0.15% Polymer in solution	73.0	0.00	100.0
Yolo loam from West Los Angeles, Calif.			
Control	0.0	4.45	
Level 1	5.6	1.11	75.0
Level 2	11.2	0.33	92.6
Level 3	16.8	0.08	98.2
0.1% Polymer in solution	33.6	0.00	100.0

Several uses of the polyacrylamide polymers for soil erosion control are possible, and practical research must be continued for a number of years on each of these.

On hillsides where rain or irrigation cause surface runoff with gullying or other types of soil movement, polymers can be mixed into the soil at various depths. This will increase infiltration into soil and give more time for rainwater or irrigation water to percolate to different depths and thus decrease the chance for soil erosion. In some cases the polymer can increase the water-holding capacity of the soil. This method of erosion control can lead to soil becoming saturated, which happens when infiltration is high to given depths. If the incline is great enough, the weight of the saturated soil could cause slippage, although this is less likely when there is no imported soil. The greater the depth of treatment, the greater the amount of water that can be stored in the soil and retained for deep percolation.

In another procedure, conditions are the same as for above except that the polymer is supplied only to the surface 1 to 3-cm depth. This is best done with sprinkler irrigation; 0.5 to 1.5 cm of water would be needed. This will also increase infiltra-

tion, but perhaps at a slower rate than above. Under intense rain there then would be the possibility of some runoff, but the stable aggregated soil surface would have a decreased tendency to move. This controlled runoff would decrease the chances of having supersaturated soil that could slip under some conditions, especially when fill soil is involved. Effects can be controlled by the concentration of polymers in the irrigation water; a useful range could be 1 to 500 mg L⁻¹.

Another procedure involves spraying polymers in solution or applying dry polymers followed by wetting onto the soil surface. After drying, the stable structure of the surface of soil will not easily break during rain, even though water will penetrate, but with much running off. The soil should not be cultivated in this situation. Another procedure involves applying polymers to soil via irrigation water to decrease soil erosion by the irrigation water, particularly from furrows. Still an other procedure involves applying polymers to open fields to decrease erosion of dust by wind (Chepil 1954).

AMELIORATION OF SODIC SOILS WITH POLYMERS

Sodic soils generally have poor physical properties (Gupta and others 1984; Helley 1937; Richards 1954), and this leads to poor plant growth and makes land reclamation difficult. A high sodium adsorption ratio, a high soil pH, and simultaneously high levels of CaCO₃ contribute to the dispersion behavior of soils that give poor aeration, poor water intake, poor drainability, and that resist cultivation. Under unfavorable conditions, even humic substances can enhance dispersion of soil (Gupta and others 1984). Swelling contraction of certain clays under sodic conditions and low salt water also contributes to poor physical properties of soil (Aldrich and Schoonover 1951; Gupta and others 1984; Helley 1937).

Any means of increasing the soluble Ca in the soil does improve the characteristics of sodic soils (Aldrich and Schoonover 1951; Richards 1954). Gypsum, soluble CaCO₃, and acidifiers of calcareous soils can improve sodic soils. Associated leaching is essential; but at least initially, this is difficult to achieve.

Quastel (1954) pointed out that the soil conditioner CRD-186 (Allison and Moore 1956), when applied to alkaline and saline soils, facilitated the removal of salt and exchangeable Na with irrigation. In the Soviet Union, Khamraev and others (1983) found that the structure of alkaline-sodic soils was improved and that salts were more easily washed from soils when treated with a polyelectrolyte. The efficacy of the treatment increased with increasing molecular weight of polymer, and it decreased with increasing hydrolysis of the polymer. Allison (1952) and Allison and Moore (1956) showed that synthetic soil conditioners can provide stability to sodic soils.

Gardner commented that a soil conditioner must be less expensive than gypsum to be competitive (see Barrada 1972), but failed to state that quantities

must also be considered. For example, 2 to 10 kg polymer soil conditioner must be compared with from 2 to 20 MG gypsum; even so, their effects are mostly different. In the studies of Allison (1952), the polymer treatments gave manifold increases in the rate of water infiltration. Sweet corn yields were about doubled in saline-alkaline soils by the conditioners, but they had less effect on non-alkaline-saline soil. Exchangeable sodium was also decreased by the treatments.

The results of all the 35-year-old studies are valid (Wallace and others 1986). Today, however, new polymer soil conditioners and application procedures are available that can decrease by 100 or more times the rates needed to achieve the same results.

Table 2--Retention, %, of soil particles on sieves of different size openings with application of soil conditioners to a sodic soil from Lost Hills, California¹

Sieve openings	Control	56 kg Polyacrylamide ha ⁻¹
mm	% of 50 g retained, cumulative	
0.589	2.0	2.7
0.295	7.3	66.2
0.149	22.2	81.6
0.104	27.4	83.5
0.059	38.6	84.7
Bottom	100.0	100.0
	% in bottom container	
	61.4	15.3
	Δ for 0.104 sieve opening or greater	
		56.1

¹Sieves, other than control, were drenched with solution containing 0.5 mg L⁻¹ appropriate polymer.

Table 3--Time needed for infiltration of water through stabilized and unstabilized sodic soil from Lost Hills, California

Treatment rates anionic polyacrylamide kg ha ⁻¹	Infiltration time for 25 ml in 25 g soil, s	Strength of aggregates in water
0	270	Feeble
28	95	Marginal
56	70	Very good
112	45	Strong
168	45	Strong
224	45	Strong

We applied new-generation soil conditioners to sodic soils in various procedures. In flocculation tests, followed by wet-sieving, particle sizes were approximately four to five times larger with new soil conditioners than with controls (table 2). Water penetration was greatly improved on a sodic soil when conditioned with a new soil conditioner (table 3).

ENHANCEMENT OF THE EFFECT OF COAL FLY ASH BY A POLYACRYLAMIDE SOIL CONDITIONER

In producing energy by burning coal, the United States produces about 40 million MG of fly ash per year (Babu 1975; Bond and others 1972). Even though there are agricultural and reclamation uses for it as a soil amendment (Faber 1976; Hodgson and others 1972; Jastrow and others 1981; Martens and Beahm 1978; Phung and others 1978; Terman and others 1978), the supply is greater than present use. As a consequence, large quantities of it are piling up. There is some environmental hazard due to the erodibility of the stockpiles. The objective of this study was to explore the possibility of disposing of fly ash in soil more acceptable with a simultaneous treatment with a polymeric soil conditioner (Wallace and Wallace 1986), so that the high levels of fly ash do not cause the physical properties of soil to deteriorate, as has been observed when high rates of fly ash are supplied to soil (Chang and others 1977; Parker and others 1978).

We grew wheat (*Triticum aestivum* L. cv. INIA66R) in a calcareous clay soil, a Torrifluvents from Imperial Valley, California, on containers in a glasshouse. The soil was amended with 450 kg ha⁻¹ anionic polyacrylamide and 748 mg ha⁻¹ of coal fly ash in factorial combination. Both amendments increased the vegetative yield of the wheat when applied singly, and when they were applied together the effect was sequentially additive (table 4).

Table 4--Vegetative yield of INIA66R wheat grown 19 d in a calcareous clay with and without a polyacrylamide (PAM) and with and without fly ash in factorial combination

Soil treatments	Dry weight mg plant ⁻¹	Relative yield	Calculated relative yield
Control	28.5	1.00	--
450 kg ha ⁻¹ PAM	33.3	1.31	--
748 mg ha ⁻¹ fly ash	36.4	1.43	--
PAM + fly ash	49.6	1.95	1.87 ¹
LSD 0.05			

¹The combined effect appears to be sequentially additive because the product of 1.31 x 1.43 is very near the actual response for plants grown with both PAM and fly ash (1.95 versus 1.87).

Without the polyacrylamide, soil was compacted. Large quantities of waste fly ash can be disposed of with little or no environmental hazard through high-level application to land with simultaneous use of a polymer soil conditioner to maintain acceptable physical properties of soil.

CONCLUSIONS

1. Cost savings with more effective soil preparation can be achieved when polymeric soil conditioners are included in land reclamation projects.
2. Soil aggregate stability can be achieved for several years without simultaneous addition of extremely large quantities of organic amendments--modest quantities of organic amendments will do just as well as will large quantities as there are synergistic effects if applied with polymeric soil conditioners.
3. Use of polymeric soil conditioners can help overcome most of the problems related to loss of topsoil. Water penetration can be made to be satisfactory. Soil erosion can be minimized and even completely avoided. Soil becomes well aerated, and plants do better due to improved root growth.
4. Soils that drain very poorly due to such conditions as sodicity and excess salinity can be made to drain so that the reclamation process can be completed more rapidly and more efficiently than otherwise possible.
5. Polymeric soil conditioners can be important tools in the management of waste products that can be incorporated into soil in reclamation projects or of waste products for which land disposal is possible. Coal fly ash, mine tailings, and sewage sludge are examples.
6. New polymers are available for soil conditioning that are much better than those in use 35 years ago. Excellent soil preparation can be achieved with as little as 0.5% of the rates of the polymers in use then. Results are now better, and the economics is very favorable.
7. The most useful of the new polymers has been in investigation and use for the past five years.
8. The polymeric soil conditioners will improve any soil that contains some clay. The soil may be acid, neutral, or basic.
9. Soil tests are available which can predict need for and response to the polymeric soil conditioners. Soils laboratories in the past have tested soils primarily for their nutrient needs, but now it is possible to also test them for possible improvement of physical properties of soils.

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CREATING RIPARIAN WILDLIFE HABITAT ALONG A COLUMBIA RIVER IMPOUNDMENT IN

NORTHCENTRAL WASHINGTON //

Robert G. Carson and Paul J. Edgerton

ABSTRACT: Irrigated riparian plantings totaling 37.5 ha were developed to compensate for habitats lost as the result of an increase in the operating level of Rufus Woods Lake. Twenty-four species of shrubs and trees were planted to provide forage and cover for wildlife. Soil characteristics, deer browsing, grass competition, and individual species' moisture needs have influenced development of the plantings.

INTRODUCTION

During February 1981, the U.S. Army Corps of Engineers (COE) implemented a 3-m pool rise on Rufus Woods Lake (RWL), an impoundment of the Columbia River in northcentral Washington (fig. 1). The purpose of the pool rise was to provide additional electrical generating capacity. As a result, 223 ha of land were inundated, including 47 ha of riparian habitat along the perimeter of the lake (Tabor and others 1980).

Under the authority of the Fish and Wildlife Coordination Act of 1958 (Public Law 85-624), the COE mitigated for wildlife losses which resulted from the 1981 rise. Studies were conducted prior to the pool rise (Erickson and others 1977) to determine the kinds and extent of habitats which would be flooded and to survey the wildlife populations using those habitats. A committee consisting of representatives of the COE, U.S. Fish and Wildlife Service, Washington State Department of Game, and the Colville Confederated Tribes then prepared a mitigation plan (U.S. Army Corps of Engineers 1980) which was funded and implemented by the COE. A major component of the plan was the replacement of inundated riparian habitat through the planting and irrigation of

riparian tree and shrub species on upland areas adjacent to the lake. Other features of the mitigation plan not addressed in this paper included the construction of islands for waterfowl nesting and brood rearing, goose nesting structures, goose feeding pastures, raptor perch poles, and the fencing of some remaining riparian areas along the river to exclude livestock grazing.

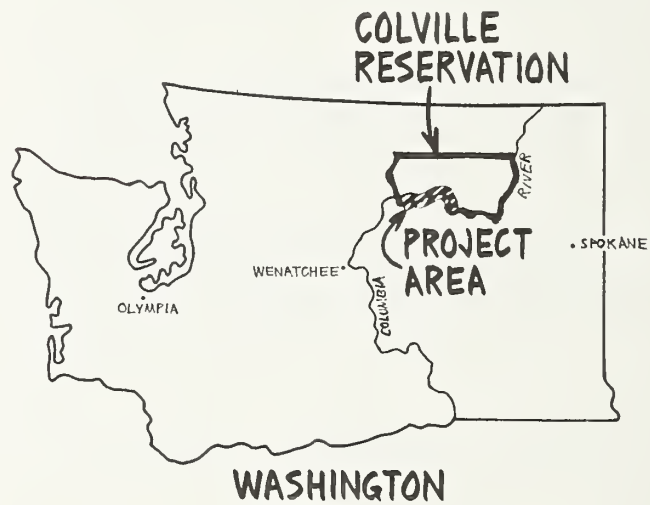


Figure 1--Location of the riparian habitat development project area along the Columbia River in Washington.

This paper describes an important operational project to develop and maintain riparian habitat through irrigation and planting. Some of the management concerns that have surfaced during the project underscore our need to better understand the ecophysiology of commonly planted wildland shrubs and trees in order to better match them to site factors and management treatments. Permission was granted by the COE, Seattle District, to publish the information contained in this paper.

PROJECT AREA DESCRIPTION

RWL is an impoundment of the Columbia River formed by Chief Joseph Dam. The reservoir extends 83 km, reaching almost to the base of Grand Coulee Dam. Width of the lake ranges from 150 m to 800 m, and maximum pool elevation is 291 m. Soils of the project area were derived

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from weathered granite, glacial outwash and alluvium, with loess deposits on the surface (Beielser 1981).

The climate is characterized by hot, dry summers and cool, dry winters. Average temperatures at the Chief Joseph Dam weather station range from -4 to 0 °C during December through February, and 19 to 23 °C during June through August. Considerable diurnal variation in temperature occurs in all seasons with annual extremes ranging from -23 to 46 °C.

Average annual precipitation is approximately 25 cm. Average monthly precipitation during the summer is 1.40 cm. Monthly winter precipitation averages 3.15 cm with the majority occurring as snowfall.

The vegetation in the project area is typical of arid grass-shrub communities found throughout much of eastern Washington and Oregon (Daubenmire 1970, Daubenmire and Daubenmire 1968). Large areas adjacent to the reservoir are dominated by basin big sagebrush (*Artemisia tridentata* tridentata)¹ and antelope bitterbrush (*Purshia tridentata*) communities. Basin big sagebrush occurs on deep, moderately drained soils at low to mid elevations while bitterbrush occurs on deep, sandy or gravelly soils at low elevations. The most extensive habitat types are big sagebrush/bluebunch wheatgrass (*Agropyron spicatum*), big sagebrush/needle-and-thread grass (*Stipa comata*), bitterbrush/bluebunch wheatgrass, and bitterbrush/needle-and-thread grass. The giant wildrye (*Elymus cinereus*)/saltgrass (*Distichlis stricta*) habitat type occurs on alkaline sites.

RIPARIAN HABITAT DEVELOPMENT

Construction of six irrigated riparian habitat development areas along RWL was initiated by the COE in 1982 and completed in early 1983. Each area was fenced to exclude livestock and existing vegetation was cleared using a rotary-chain mower. Depending on the size and configuration of each site, 5 to 24 irrigation circles (55 m average diameter) were constructed to utilize water pumped from RWL (fig. 2). The irrigation systems consisted of permanently mounted sprinkler heads on 1.83-m standpipes operated either individually or two at a time by either 20-horsepower or 40-horsepower submersible pumps. Water was applied at an average rate of 1.52 cm per hour. The area under irrigation at each site ranged from 1.9 to 10.9 ha with the entire project totaling 37.5 ha (table 1).

Sherman big bluegrass (*Poa ampla*) and Durar hard fescue (*Festuca ovina duriuscula*) were seeded in the fall of 1982 to establish a dense grass stand that would prevent the establishment and spread of noxious weeds. Trees and shrubs were hand-planted during April and May of 1983 at a density of 3580/ha. The desired stocking at maturity was

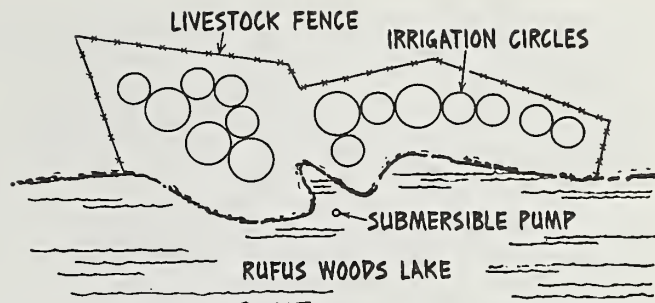


Figure 2--Typical layout of an irrigated riparian habitat area. Note that the irrigation circles vary in size.

Table 1--Area under irrigation at each of the six riparian habitat development sites

Site name	Area irrigated
	<u>Hectares</u>
Wells Flat	9.1
Brandts Landing	1.9
Arrowhead	7.3
Allen Bar	10.9
Site 12	4.6
Alameda Flat	3.7
Total	37.5

PLANTING LAYOUT FOR AN IRRIGATION CIRCLE

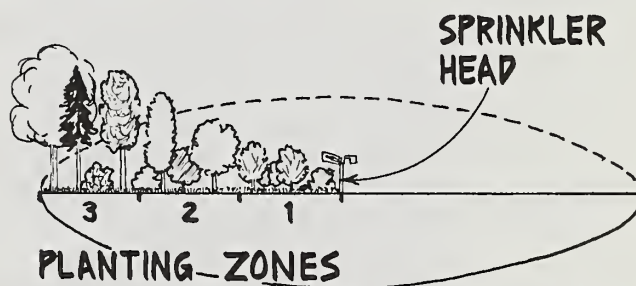


Figure 3--Typical cross-section of an irrigation circle showing the location of planting zones. The circles average 55 m in diameter.

1790/ha (assuming 50% mortality). One and 2-year-old containerized seedlings grown in 65-cc cells were planted in 0.25-m² areas scalped free of competing vegetation. A slow-release fertilizer tablet was inserted 3 cm away from the seedling roots.

Irrigation circles were divided into three concentric planting zones from the sprinkler head to the circle perimeter (fig. 3). Each zone encompassed approximately one-third of the irrigated area. Species were planted in specific

¹Scientific and common names are from Garrison and others (1976) and Plummer and others (1977).

zones according to expected maximum height at maturity. Low growing shrubs were planted closest to the sprinkler head, and trees and tall shrubs were planted closest to the perimeter. The purpose of this planting design was to ensure that all plants received a sufficient amount of water throughout the duration of the project.

More than 100,000 seedlings, including three conifer species, five deciduous tree species, and 16 deciduous shrub species (table 2), were planted during the spring of 1983 to provide similar forage value and structural diversity to that of the inundated habitats. An additional

21,000 seedlings were planted during April 1984 to replace first-year mortality and to adequately stock areas missed during the initial planting.

Irrigation provided supplemental water throughout the typically warm, dry growing season. During the 1983-86 seasons, approximately 3.5 cm of water were applied weekly beginning about the third week of April and continuing through late August (fig. 4). Irrigation was terminated in late August to allow gradual drying of the soil and to induce dormancy prior to the onset of harsh, winter temperatures.

Table 2--Tree and shrub species planted during 1983 and 1984 in irrigated riparian habitats developed along Rufus Woods Lake, Washington

Common and scientific names	Number planted
Coniferous trees:	
Ponderosa pine (<u>Pinus ponderosa</u>)	2,645
Rocky Mountain juniper (<u>Juniperus scopulorum</u>)	2,615
Colorado blue spruce (<u>Picea pungens</u>)	2,369
Subtotal	7,629
Deciduous trees:	
Russian-olive (<u>Elaeagnus angustifolia</u>)	5,506
Black locust (<u>Robinia pseudo-acacia</u>)	2,395
Black cottonwood (<u>Populus trichocarpa</u>)	1,487
Water birch (<u>Betula occidentalis</u>)	1,291
Mulberry (<u>Morus</u> sp.)	485
Subtotal	11,164
Deciduous shrubs:	
Native rose (<u>Rosa</u> sp.)	23,372
Common snowberry (<u>Symphoricarpos albus</u>)	18,995
Golden currant (<u>Ribes aureum</u>)	12,830
Blueberry elder (<u>Sambucus cerulea</u>)	12,035
Smooth sumac (<u>Rhus glabra</u>)	8,910
Red-osier dogwood (<u>Cornus stolonifera</u>)	7,250
Black hawthorn (<u>Crataegus douglasii</u>)	6,779
Himalayan blackberry (<u>Rubus discolor</u>)	5,410
Serviceberry (<u>Amelanchier alnifolia</u>)	3,237
Huckleberry (<u>Vaccinium</u> sp.)	1,085
Skunkbrush sumac (<u>Rhus trilobata</u>)	620
Western virginsbower (<u>Clematis ligusticifolia</u>)	620
Buffaloberry (<u>Shepherdia</u> sp.)	575
Common chokecherry (<u>Prunus virginiana</u>)	500
American plum (<u>Prunus americana</u>)	320
Bush cinquefoil (<u>Potentilla fruticosa</u>)	135
Subtotal	102,673
Total all species	121,466

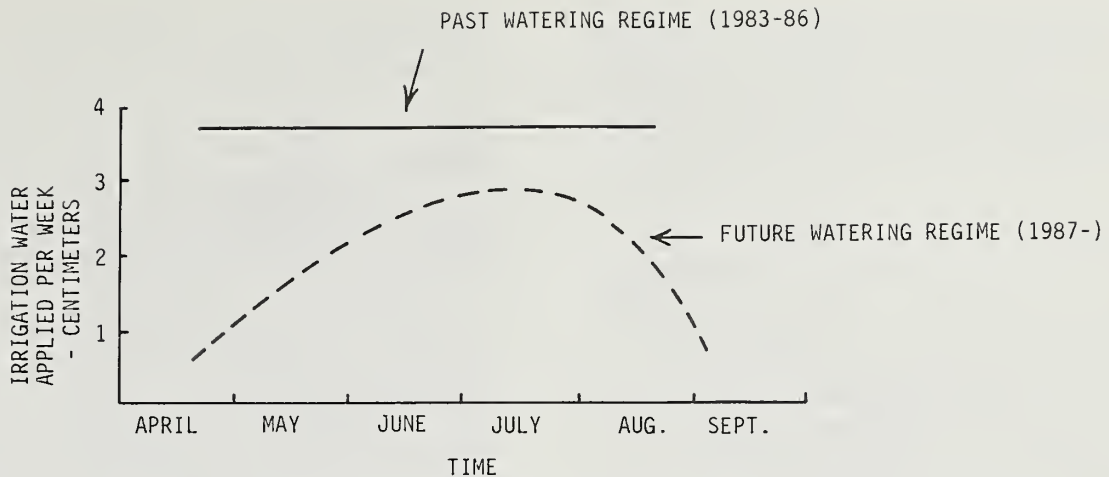


Figure 4--Past and present watering regime showing the seasonal distribution of the amount of irrigation at an average site.

RESULTS AND DISCUSSION

The results of studies currently in progress to provide detailed information on survival and growth of individual species are not yet available. However, based on extensive observations, we estimate that overall survival of shrubs and trees after five growing seasons is approximately 80 percent. In some areas, there has been virtually no mortality, whereas in localized areas where alkalinity is high or other soil characteristics are unfavorable, survival has been poor. Growth rates of shrubs and trees have varied greatly both between and within the six irrigated areas, and between species. Four major factors appear to be affecting growth rates: soil characteristics, water requirements of individual species, grass competition, and deer browsing. There appears to be considerable interaction among these factors, thus complicating the assessment of their individual effects.

Soil Characteristics

Extensive soil testing was conducted within the six irrigated riparian habitat areas during 1986. Physical and chemical soil characteristics of areas where excellent shrub and tree growth occurred were used as baselines to evaluate those areas where growth was poor. Although considerable variation occurred between sites, poor growth was generally correlated with deficiencies of important soil nutrients such as nitrogen, potassium, or sulfur. There is concern that continued irrigation of these relatively infertile soils may be leaching nutrients from the root zone, particularly on coarse, sandy soils. Test applications of fertilizer are proposed for the fall of 1987. If positive responses are observed, large-scale fertilizer applications may be implemented in 1988.

Poor plant growth in areas with adequate soil nutrient levels appeared to be related to restrictive physical properties of the soil. Robust, fast-growing plants were often found growing in back-filled areas which had been excavated when the irrigation system was installed. Plants growing adjacent to these areas often showed poor growth rates which we believe were due to some physical limitation of the soil, such as compaction by construction equipment or the presence of a hardpan, rather than a nutritional deficiency.

Grass Competition

The seeded grass cover has become well established with lush, dense foliage and a dense root mass. Competition with this grass cover for soil nutrients is believed to be adversely affecting growth rates of the planted shrubs and trees, especially among the slower growing species. At many sites where soil analyses indicate favorable soil conditions, shrubs and trees are growing poorly amidst vigorously growing grasses. In these instances, it appears that grasses are out-competing the shrubs and trees for nutrients, and to a lesser extent, are reducing available sunlight.

Benefits of the dense grass cover may outweigh competitive effects. The grass cover provides habitat for several species of small mammals and birds and has effectively prevented the establishment of noxious weeds which are of great concern to agriculturalists and public land managers in the area. Numerous small areas which were missed during grass seeding operations in 1983 were rapidly colonized by annual and perennial forbs such as Canada thistle (*Cirsium arvense*), horseweed (*Conyza canadensis*), yellow sweetclover (*Melilotus alba*), and tumbled mustard (*Sisymbrium altissimum*). These plants compete aggressively for nutrients, moisture and sunlight and, in areas where they were particularly dense, may have contributed to the mortality of some tree and

shrub seedlings during the first growing season. In areas that were seeded with grasses, however, these noxious weeds were uncommon by the end of the second growing season. In most areas the grasses have not significantly affected shrub and tree growth, and have generally been beneficial to the development of the riparian habitats.

Test applications of Kerb herbicide (3,5-dichloro-N-benzamide) were made in November 1986 in localized areas where the seeded grasses appeared to be adversely affecting tree and shrub growth. Kerb selectively kills grass but does not affect broadleaf plants or conifers. Favorable results were observed during the spring of 1987 with nearly 100-percent grass kill within the 0.75-m diameter treated spots. The herbicide did not appear to be toxic to any of the planted trees and shrubs. We anticipate that the treated plants will not only benefit from the release from competition, but also from nutrients and organic matter added to the soil as the foliage and roots of the treated grasses decompose.

Water Requirements

The 24 species of shrubs and trees planted are native to environments with a wide range of moisture regimes. Ponderosa pine, serviceberry, snowberry and several other species are native to mesic, upland sites within the project area. Accordingly, they require much less supplemental water than true riparian species such as water birch or black cottonwood.

Neither the effects of overwatering nor the minimum water requirements for many of the planted tree and shrub species are well understood. Since the time of planting in 1983, all species have been watered at the same rate throughout the growing season. This practice has been sufficient to allow establishment and growth of the most water-loving species without any obvious negative effects on those species that require less water. It would be beneficial, nevertheless, to develop a watering regime that promotes optimum growth of most species without overwatering. It is likely that overwatering reduces growth rates by leaching soil nutrients from the surface soil horizons. In addition, excessive watering increases manpower and equipment maintenance costs.

Beginning with the 1987 season, a watering regime was implemented that was responsive to the seasonal pattern of available soil moisture and to the peak moisture demands of the shrubs and trees. Soil moisture levels were monitored closely and water was applied to just saturate the soil profile. Between irrigations, the soil was allowed to dry almost to the point of causing moisture stress. This resulted in approximately a 35-percent decrease in the amount of irrigation applied. The watering schedule throughout the irrigation season was also altered, with less water applied in spring when the soil profile was charged from snowmelt, and more applied in mid-summer when evapotranspiration was greatest (fig. 4). This watering regime is proposed for future years to reduce nutrient leaching and promote deeper rooting of shrubs and trees.

Deer Browsing

Deer browsing has been a major factor affecting growth and survival of the planted shrubs and trees at several sites. Mule deer (*Odocoileus hemionus*) utilize most of the areas on a yearlong basis, with greatest concentrations occurring during wintering periods. Unlike the other factors previously discussed, deer browsing is easily recognized and measured, and can be controlled by fencing and other means.

From 1983 to 1986, yearlong heavy browsing significantly affected the development of shrubs and trees at Allen Bar, while the other five riparian habitat development areas received little to moderate browsing pressure. By 1986, few plants at Allen Bar were taller than 20-25 cm, while average heights at other sites probably exceeded 100 cm. Species receiving the heaviest use, such as red-osier dogwood, black cottonwood, black locust, and water birch, experienced considerable mortality (>50%). To prevent continued mortality and deterioration of habitat quality, a temporary deer-proof fence was constructed around the area in 1986. In addition, the site was replanted in April 1987 with 14,000 tree and shrub seedlings to compensate for mortality incurred during 1983 to 1986. Surviving shrubs and trees from the original planting have exhibited excellent growth since deer have been excluded. The fence will be removed in 5-10 years when the plants are large enough to withstand the impact of heavy deer browsing.

Promising Species

After five growing seasons, 11 species have been quite successful based on their survival and growth, and use by wildlife for forage or cover. Trees include ponderosa pine, Rocky Mountain juniper, black cottonwood, black locust, Russian olive, and water birch; shrubs are golden currant, Himalayan blackberry, rose, common snowberry and red-osier dogwood. Other species are likely to become more important as they become better established or respond to management practices such as fertilization, release from competition, or protection from deer.

CONCLUSIONS AND RECOMMENDATIONS

After five growing seasons, a variety of trees and shrubs have become established in the riparian habitat development areas. They include true riparian species such as water birch, and others such as black locust and Russian olive that require less moisture but cannot grow satisfactorily in the arid shrub-steppe environment without supplemental water. Although the plantings are still developing, the most successful areas (and species) have already begun to emulate the structure and function of the riparian habitats they were developed to replace.

Numerous wildlife species are using the plantings, including mule deer, waterfowl, upland game birds, song birds, small mammals, and reptiles. A

variety of raptors perch and capture prey in the plantings. As the riparian habitats continue to develop, utilization by wildlife is expected to increase.

As a result of the experience gained to date from this project, we recommend that several important factors be considered in the development of similar projects to maximize their present and future value to wildlife. First is size and location of wildlife habitat management areas in relation to existing, planned, and potential adjacent agricultural developments. Along RWL, the land surrounding several of the irrigated sites has been converted from shrub-steppe vegetation to intensively managed agricultural fields and fruit orchards. This has precluded the use of these areas by many wildlife species that either avoid human activity or are excluded by fences or other physical barriers.

The spatial distribution of replacement habitat is also an important consideration. The number of hectares of riparian habitat that were created by this project closely approximates the number that were inundated by the 1981 pool rise. However, the distribution of the riparian habitat that was inundated (long, narrow bands along many kilometers of river shoreline) is vastly different from that which was developed for mitigation (several large blocks). This may have either positive or negative impacts on wildlife depending on habitat use patterns and the size of the home range or territory required by individual species.

Next is the need to lessen or exclude grazing and browsing pressure on young plants to allow establishment. This may require short-term fencing where seasonal livestock grazing or wintering concentrations of big game are likely to suppress growth or cause unacceptable seedling mortality.

It is also important that the wide range of growth requirements of the various species planted be considered when developing maintenance procedures for this kind of project. This includes the formulation and close monitoring of an appropriate irrigation schedule, application of supplemental nutrients (fertilization), and mechanical or chemical control of competing grasses and forbs. In some situations, carefully controlled grazing and prescribed fire may be appropriate strategies to suppress competition.

Finally, it is critical that an adequately funded monitoring program be incorporated into the project. This will help to identify problems that may arise and will ensure that project goals are being met. A monitoring program will also allow people involved in the planning or operation of similar projects to learn from others' successes and failures. The project described in this paper has been an effective but costly means of mitigating for habitat losses along RWL. Where limited funding is available, however,

managers and biologists should consider alternative strategies such as shoreline plantings, protection of existing riparian communities from grazing, development or enhancement of riparian habitat around springs and along small streams, and the installation of other less expensive supplemental watering systems.

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USE OF NATIVE SHRUBS ON STRIP-MINED LANDS IN THE HUMID EAST //

H. Glenn Hughes

ABSTRACT: Past and present factors limiting shrub use on mined lands are reviewed. Competing herbaceous vegetation on strip-mined sites in Pennsylvania hindered woody plant growth and survival. Reclaiming sites of high productive potential with shrubs valuable to wildlife requires reduction of herbaceous competition. One-time herbicide treatments generally do not work, multiple herbicide applications are economically unfeasible in most situations. Seeding or planting shrubs in strips devoid of herbaceous species may increase shrub survival by decreasing competition.

INTRODUCTION

Reclaiming strip-mined areas represents an opportunity for the establishment of shrubs and other vegetation as wildlife habitat because whole ecosystems are constructed. However, strip-mined areas contain a variety of site characteristics, due principally to the evolution of reclamation laws which began around World War II. Early reclamation efforts were concerned primarily with steep slopes, highwalls, and physical hazards, but as laws and regulations progressed more attention was focused on revegetation.

In 1977 the Federal Government passed legislation establishing minimum requirements for reclamation of mined lands (Leedy and others 1981). This legislation requires, among other things, the separation and replacement of topsoil, restoration of land to approximate original contours, and establishment of perennial vegetation. While this legislation reduced soil erosion and sedimentation, the use of perennial woody species, including shrubs, has decreased. Meeting bond requirements by achieving a certain percentage of perennial plant cover is easier with herbaceous species than with woody species (Vogel 1979). Additionally, herbaceous vegetation used on mined sites is typically more aggressive than woody species and hinders woody plant growth and survival (Davidson and others 1984). Also, soil compaction from grading is detrimental to woody perennials (Chapman 1967) and can restrict root growth and development (Spaniol 1982).

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In this paper I examine the use of shrubs on re-claimed sites, the factors limiting shrub growth and survival, ways to increase revegetation success using shrubs, and the future role of shrubs for strip-mining reclamation. Due to the drastic differences between past and present mine site conditions, revegetation failures of the past may not occur under present conditions. Likewise, revegetation successes of the past may not be repeatable.

FACTORS LIMITING SHRUB USE

Historically, site characteristics such as acidity, fertility, or soil depth have limited the development of vegetation on eastern mined sites (USDA Soil Conservation Service 1978). Consequently, species which survived on these sites (and recommended for reclamation purposes) were those which could tolerate adverse site conditions. Shrubs typical of this category include bristly locust (*Robinia fertilis*), autumn olive (*Elaeagnus umbellata*), multiflora rose (*Rosa multiflora*), Japanese barberry (*Berberis thunbergii*), Japanese honeysuckle (*Lonicera japonica*), and tartarian honeysuckle (*L. tatarica*) (Leedy and others 1981). Primarily exotics, some of these species escaped into adjacent areas, proving difficult to control and decreasing site productivity (i.e., multiflora rose, Japanese honeysuckle and, to a lesser extent, autumn olive). Studies using native shrubs have not been promising. In a guide compiled by the USDA Soil Conservation Service (1978), few of the native shrub species extensively tested (10+ sites) performed well. Other factors can also limit the use of shrubs on strip-mined lands such as browsing by wildlife, particularly deer and rabbits, seed availability and germination, and slow growth rates.

With the advent of the 1977 legislation, liming and fertilization became common practices to reduce acidity and increase nutrient levels. Additionally, regulations required the establishment of 70% perennial plant cover by the mining company for release of its bonding obligation. The primary objective of current reclamation practice is the establishment of perennial herbaceous species such as K-31 tall fescue (*Festuca arundinacea*), birdsfoot trefoil (*Lotus corniculatus*), and crownvetch (*Coronilla varia*) which rapidly meet the 70% cover requirement. Shrubs or trees are a secondary consideration, if planted at all. In addition, species such as tall fescue may suppress slow growing woody species (Leedy and others 1981). Consequently, over the past 10-15 years, factors limiting the use of shrubs possibly changed from site attributes (low pH) to increased herbaceous competition.

Currently, species recommendations for mine reclamation in the Eastern United States are based largely on tolerance to infertile and acid sites (USDA Soil Conservation Service 1978). Studies on rights-of-way have indicated that herbaceous vegetation effectively controls shrub growth and survival (USDA Plant Materials Center 1978, 1985). However, similar information describing how shrubs respond to herbaceous competition on strip-mined sites, and how to best alleviate competition, is not widely available. Therefore, in 1984 I began studies to evaluate shrub survival under various levels of herbaceous competition.

NATIVE SHRUB SURVIVAL

The first study examined 2 native shrubs, silky dogwood (*Cornus amomum*) and northern arrowwood (*Viburnum recognitum*), as potential shrub species for use on strip-mined sites and the effects of herbaceous competition and deer browsing on plant survival. The effects of 3 levels of herbaceous competition (low, medium, and high) on shrub growth and survival were tested.

The high level of herbaceous competition was produced by planting shrubs onto a site already supporting K-31 tall fescue and birdsfoot trefoil. The medium level of herbaceous competition was produced by spot application of a non-selective herbicide (Roundup brand of glyphosate) on a site supporting herbaceous vegetation and planting shrubs in the bare spots created by the herbicide. The low level of herbaceous competition was produced by planting seedlings immediately after herbaceous species were seeded. Exclosures were erected on approximately 20% of each area to evaluate deer impact.

The effects of herbaceous competition and species on shrub survival after two years were analyzed with log-linear analysis of survival probabilities (SAS 1982: 257-285). Although shrub survival was high after 1 growing season (78-98%), data after the second (and drier) growing seasons indicated that survival dropped considerably (table 1). This resulted from poorer growing conditions (less rainfall) in 1985 and increased herbaceous cover in those treatments either sprayed or planted at the time of seeding. Both species and level of herbaceous competition affected survival after two growing seasons (Chi-square = 78.4 and 54.4, respectively, $p < .01$). However, more recent data indicate that survival on most treatments is now below 50%. Apparently, control of herbaceous competition is needed for several years to ensure adequate survival of these shrubs.

Table 1--Percent survival of silky dogwood and northern arrowwood under 3 levels of herbaceous competition at 1 and 2 growing seasons after planting (1984/85)

Species	Herbaceous Competition		
	Low	Medium	High
Silky dogwood	70	56	48
Northern arrowwood	76	81	74

It was evident at the end of the 1984 growing season that the herbaceous vegetation at all 3 treatment levels was competing with the shrubs for water and nutrients. Spot application of herbicide, though reducing herbaceous vegetation temporarily, did not prevent herbaceous species, particularly clover, from invading the sprayed area later in the growing season. Likewise, where shrubs and herbaceous vegetation were planted concurrently, herbaceous vegetation became established quickly.

DIRECT SEEDING

Due to the rapid establishment of herbaceous vegetation and subsequent effects of competition on shrubs in the above study, another study was begun in 1985 to examine alternative ways to reduce herbaceous competition. Herbaceous species are frequently planted by drilling. This technique was modified to reduce competing herbaceous vegetation and enhance growth and survival of woody species. Instead of spraying existing herbaceous vegetation or planting seedlings into freshly seeded sites, the intent was to test a system where both herbaceous and woody species could be seeded in one pass. To decrease competition, the seeding procedure was modified to seed woody species in one port and herbaceous species in the other ports of the Tye Pasture Pleaser planting drill. This required plugging certain ports in the drill to create a bare strip in the herbaceous seeding (table 2).

Scarified black locust (*Robinia pseudoacacia*) seeds were planted in the bare strips, thus reducing the effects of herbaceous competition. Black locust, though not a shrub, was used because it is perhaps the most successful and commonly used woody species in Pennsylvania on strip-mined sites and could be expected to survive relatively well. Any differences in survival or growth would then be due to the planting procedure.

Table 2--Seeding design used on the Tye Pasture Pleaser to achieve high, medium and low levels of herbaceous competition when seeding herbaceous and woody species¹

Level of competition	Seed box	Port number									
		1	2	3	4	5	6	7	8	9	10
High	Large	20	0	0	0	0	0	0	0	0	-
	Small	0	0	0	0	L	0	0	0	0	-
Medium	Large	0	0	0	0	-	0	0	0	0	-
	Small	0	0	0	0	L	0	0	0	0	-
Low	Large	0	0	0	-	-	-	0	0	0	-
	Small	0	0	0	-	L	-	0	0	0	-

¹The large seed box contained tall fescue, and the small seed box the legume mixture and black locust.

²0=open; L=locust; --closed

The drill used was a 10-port Tye Pasture Pleaser, with the ports 20 cm apart. The large hopper seeded K-31 tall fescue at a rate of 56.0 kg/ha. The small (legume) hopper seeded both a herbaceous mixture and black locust. Birdsfoot trefoil was the main component of the herbaceous mixture (7.1 kg/ha). The legume seed box was modified to seed black locust in the #5 port and the herbaceous mixture in the other ports.

Three different planting treatments were tested. The treatments differed in the degree of competition between locust and herbaceous species. In the first treatment, no bare strip was created, thus K-31 tall fescue and black locust were seeded in the same row, creating direct competition between fescue and black locust. In the second treatment, herbaceous species were excluded from direct competition with locust by not planting fescue in the #5 port. In the third treatment, herbaceous species were excluded from the row in which locust was seeded (#5) and from adjacent rows (#'s 4 and 6). These treatments were achieved with only minor modifications to the drill, the principal modification being the construction of a "mini-hopper" around port no. 5 to contain the locust seeds.

Sixteen months after seeding, measurements were taken on plant height, canopy cover, and number of plants per 20 m strip. At this time the site met the requirements (70 percent plant cover) for bond release.

Direct competition between herbaceous species and black locust decreased the number of live plants per plot, average plant height, and canopy cover (table 3) (Hughes and Garthe, in press). Seedling height decreased with increasing herbaceous competition. Significant differences in seedling height were noted between low and high levels of competition, but the medium level of competition was not different from either the low or high level of competition. Canopy surface area, maximum crown diameter, and minimum crown diameter results paralleled those of plant height. The level of herbaceous competition affected locust survival. The number of locust seedlings present 16 months after planting dropped dramatically when there was direct competition between herbaceous and woody species. The number of plants per plot under low and medium levels of competition was 2.5 to 3 times greater than under the high level of competition.

Some states require that a certain number of trees or shrubs be established on a reclaimed area. Kentucky, for example, requires 1,976 trees/ha (Rafail and Vogel 1978). In the current experiment, the low and medium levels of herbaceous competition meet this requirement (3,634 and 4,126 trees/ha, respectively). However, locust would have to be seeded in an additional port to achieve adequate stocking under the high level of herbaceous competition (currently 1,421 trees/ha).

These results demonstrate that even the most effective and widely used woody perennial is affected by herbaceous competition, but planting procedures can be designed to promote growth and survival of woody perennials. Seeding herbaceous and woody species in such a manner costs considerably less than planting seedlings and allows for an efficient mechanism to regulate competition between woody and herbaceous plants.

CONCLUSIONS

The future role of shrubs in reclamation in the East is uncertain. Shrubs such as bristly locust can and will be used on orphan mines with site limitations and little competing vegetation. However, the inherent low fertility limits productivity from a wildlife habitat standpoint. Lands which are mined, backfilled, graded, topsoiled, limed, fertilized, and seeded have a much higher productivity potential, but aggressive herbaceous vegetation limits shrub survival. Expecting shrubs less competitive than black locust to survive under high levels of herbaceous competition is unreasonable. Reducing competition for at least 2-3 years is required for the successful establishment of shrubs. Although this cannot be accomplished by a one-time application of herbicide, periodic herbicide application is possible, though economically unfeasible in most situations. Establishing shrubs by direct seeding has potential for reducing herbaceous/woody species competition.

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Table 3--Mean black locust growth and survival under low, medium, and high levels of herbaceous competition¹

Level of Compet.	Plant height (cm)	Maximum canopy diam. (cm)	Minimum canopy diam. (cm)	Canopy surface area (cm ²)	Number trees/plot
Low	49.9 (1.7) ^{2a}	28.1 (1.0) a	19.5 (1.4) a	435 (41) a	13.3 (1.5) a
Medium	41.3 (2.3) ab	24.2 (1.1) ab	18.3 (0.6) ab	351 (27) ab	15.1 (1.0) a
High	37.1 (4.7) b	20.8 (3.0) b	14.1 (2.0) b	260 (64) b	5.2 (1.0) b

¹Numbers within parentheses are standard errors of the means.

²Numbers within a column followed by the same letter are not significantly different (P<0.05).

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Section 3—Ecophysiology

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INFLUENCE OF STRESS HISTORY ON WATER USE PATTERNS OF HONEY MESQUITE //

R.J. [Ansley, P.W. [Jacoby and B.K. [Lawrence

ABSTRACT: Transpirational water loss by honey mesquite (Prosopis glandulosa Torr.) adversely affects watershed supply on over 23 million ha of Texas rangeland. The objective of this study was to determine response of this species to moisture availability following preconditioning to different levels of moisture stress. Twelve trees, located 20 km south of Vernon in North Central Texas, were manipulated through the use of drip irrigation and subcanopy rain shelters to three levels of moisture stress: low (LS), control (CT), and high (HS). The root system of each tree was containerized with a 2m deep vertical barrier to eliminate competition from neighboring trees and prevent lateral flow of soil moisture into sheltered areas. Predawn leaf water potentials (PWP) were -1.6, -1.2 and -1.0 MPa on June 27, and -2.1, -1.7 and -1.4 MP on July 28, 1986 for HS, CT and LS trees, respectively. Diurnal stomatal conductance (CS) was greatest on the LS trees and least on the HS trees on both dates. Following watering of all trees (equivalent to 40mm precipitation per tree) on July 29, PWP increased to similar levels in all trees but increase to maximum CS was delayed in HS trees, suggesting that prolonged moisture stress inhibited ability to recover.

INTRODUCTION

The ability of Prosopis glandulosa to resist drought and yet respond rapidly to short-term increases in soil moisture from rain showers gives it a competitive advantage over associated plant species. Under most conditions Prosopis will maintain rather than shed leaves during drought and carry on active photosynthesis and leaf transpiration during a time when associated herbaceous species are dormant. This mechanism to resist drought has been attributed to the ability of Prosopis root systems to access permanent or semi-permanent ground water supplies (Nilsen and others 1981). However, in regions such as the Rolling Plains of north central Texas where ground water is unavailable and plants must depend almost entirely on soil moisture in the surface horizons, Prosopis still

maintain a full complement of leaves during all but the most severe droughts. Rolling Plains Prosopis invest more into lateral root growth than a tap root; and previous studies indicate that as dehydration of Prosopis increases dependence on lateral roots increases (Ansley and Jacoby 1986; Heitschmidt and others 198-). Prosopis in this region appear to be highly adapted toward maximizing use of moisture which becomes available in surface soil horizons following brief summer rain showers. It is not known how quickly Prosopis respond to a rainfall event and whether the condition of Prosopis, in terms of level of moisture stress, affects the plant's ability to respond.

We hypothesize that Prosopis in the Rolling Plains maximize use of water when it becomes available. The amount of water used is dependent on the amount available. Overall condition of the plant with respect to level of moisture stress may modify response to a moisture event in terms of plant water use activity. The objective of this study was to quantify rapidity, magnitude and duration of water use response of Prosopis to a moisture event when plants are in different initial levels of moisture stress.

MATERIALS AND METHODS

Site Description

Studies were conducted on the W.T. Waggoner Estate located 20 km south of Vernon in the northern Rolling Plains ecological area of Texas. Average annual precipitation is 65 cm, which occurs on the average in a spring/fall bimodal pattern. The clay loam range site supports primarily warm season grasses and forbs dominated by a moderate overstory (<30%) of Prosopis and lotebush, Ziziphus obtusifolia. Components of the understory include: Buchloe dactyloides, Bouteloua curtipendula, Digitaria californica, Aristida wrightii, Stipa leucotricha, Opuntia phaeacantha, O. leptocaulis, and Xanthocephalum dracunculoides.

Soils of the study area are Typic Paleustolls of the Deandale and Kamay series. Both soils have developed from redbeds or old alluvium and differences between the two are related to changes in topographic micro-relief. Deandale soils form where water tends to accumulate, whereas Kamay soils generally shed water to lower lying areas. Deandale soils tend to maintain a higher and more consistent moisture content throughout the soil profile than the Kamay soils, which become progressively drier with depth.

Paper presented at the Symposium on Shrub Ecophysiology and Biotechnology, Logan, UT, June 30-July 2, 1987.

R.J. Ansley is Postdoctoral Research Associate, P.W. Jacoby is Professor, and B.K. Lawrence is Technician, [Texas A&M Agricultural Experiment Station, Vernon, TX.]

Site Preparation

Twelve multistemmed *Prosopis* trees were selected as experimental units from the overstory component of the study site on the basis of uniformity in canopy shape and basal stem number. Plant shapes were selected to follow that of a parabolic frustrum to facilitate construction of subcanopy rain shelters. Trees were 3.0-3.5m in height with canopies of 4-6m diameter at the widest part.

All woody vegetation including nonexperimental *Prosopis* occurring within 10 m of each experimental tree was removed by chainsawing aerial portions and saturating remaining plant bases with diesel oil. Each experimental tree was containerized with a sheet metal and plastic vertical barrier to a depth of 2.5m. Containerization is described by Ansley and others (1988). Four 2m long x 5cm diameter aluminum access tubes were installed within each root container at 2m laterally from tree center for soil moisture measurements at 30cm vertical intervals using the neutron attenuation method (Greacen 1981).

Treatment Installation

Root containerization, irrigation, and rain shelters were used to generate surplus and reduced soil moisture levels available to *Prosopis*. Trees exposed to natural rainfall only were selected as the controls. Additional moisture was made available through trickle irrigation for the surplus treatment, and a reduced moisture level was created by installing a sub-canopy rainout shelter as the third treatment (Jacoby and others 1988). All twelve trees were equipped with a trickle irrigation system via underground polyvinyl chloride (PVC) tubing connected to a 23,000 L tanker and electric pump powered by a 4.5 kw generator to allow application of artificial moisture events. Water from a municipally approved drinking system was supplied via water truck to the tanker.

Stomatal Conductance and Water Potential

Stomatal conductance of adaxial leaflet surfaces was measured using two LICOR LI-1600 Porometers (LICOR Inc., Lincoln, NE). Porometer readings were taken on the northeast (NE) and southwest (SW) aspects of each of the twelve trees. It was determined in an earlier study that these aspects represented the least and most stressed, respectively, with respect to ambient exposure during a typical summer day. Two porometer readings were made per aspect during each sample period which occurred at 2, 5, 8 and 11 hours post sunrise (HPS). Duration of each sample period was about 1 hour. A sampling sequence was used that would prevent confounding of treatment effects with time should activity of the trees change during the sampling period. All readings were made on predominantly clear days. Only leaves on the perimeter of each canopy were sampled.

Leaf water potential was measured using a Scholander-type pressure bomb at predawn, and during porometer sampling periods. Two leaves were excised from the center of each canopy at 1.5-2m height and water potential determined in accordance with methods outlined by Turner (1981).

Photosynthetically active radiation (PAR, 400-700nm) was determined using a LICOR LI-190S-1 Quantum Sensor at each point where conductance was measured. Two PAR readings were taken, one with the sensor oriented vertically and a second with the sensor at leaf angle facing away from the basal center of the tree. PAR values reported in this study represent an average of the two readings.

Experimental Design

The conceptual strategy of this study was to manipulate *Prosopis* to different levels of moisture stress during the same growing season, then periodically expose all trees to the same moisture event and monitor responses (fig. 1). Because of a slight variation in soils across the study site, experimental trees were assigned treatments to conform to a randomized complete block design which included four blocks of three trees each. One block contained Deandale soils and the other three contained Kamay soils. Treatments within each block were designed to produce three levels of moisture stress as described earlier; thus, each of the three stress treatments was applied to four trees.

RESULTS AND DISCUSSION

Ambient Conditions

Air temperature, relative humidity (RH) and PAR values indicate that ambient conditions were similar on each of the sample days in 1986 (fig. 2). The most stressful part of the day occurred

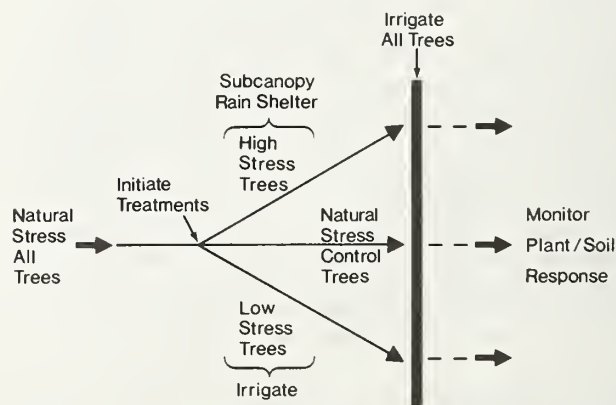


Figure 1--Schematic illustration outlining plan of the study to manipulate *Prosopis* to three levels of moisture stress, then treat all trees with an equivalent amount of irrigation, and monitor subsequent response by the trees.

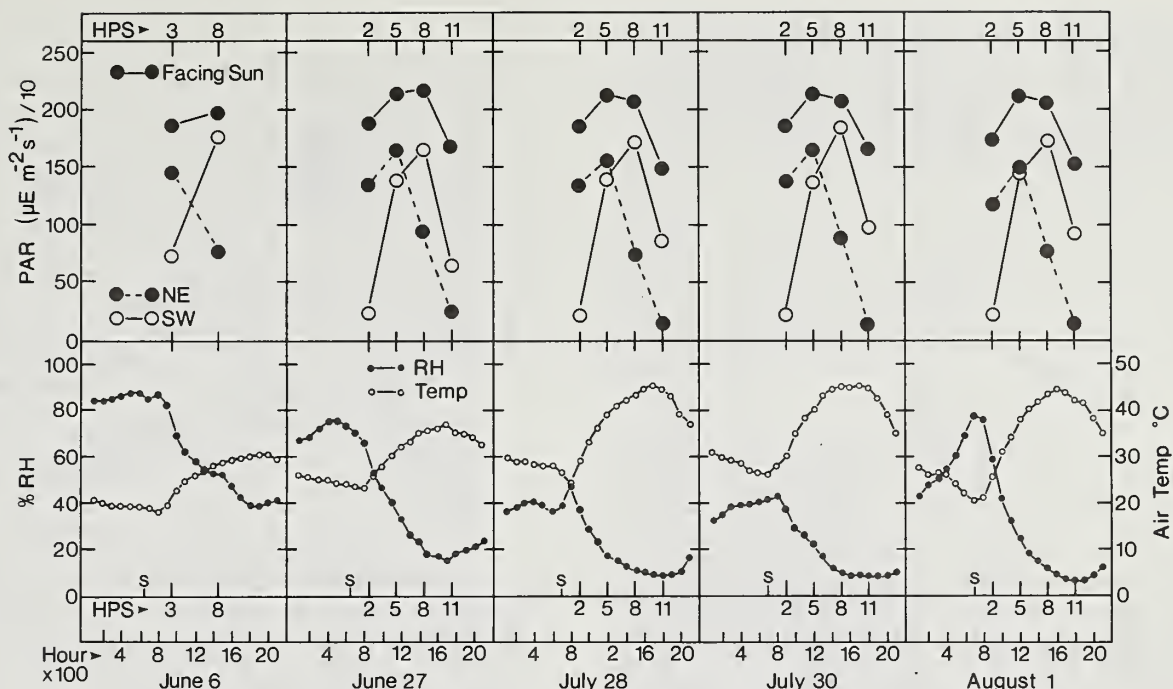


Figure 2--Photon flux density (400-700nm) facing the sun, and on NE and SW aspects of *Prosopis* canopies (top), and relative humidity and air temperature (bottom) during each of the sample days in 1986. HPS = Hours Post Sunrise, s = Sunrise.

in mid-afternoon from 8 to 11 HPS. Seasonal trends were typical in that at any HPS, RH and air temperature were greatest and least, respectively, in early June and least and greatest, respectively, in late July. Maximum PAR was similar for all sample days, indicating relatively clear and cloud free conditions. PAR changed with aspect during mornings and late afternoons, as was expected. PAR was greatest on the NE aspect early, then declined and became greater on the SW aspect by 8 HPS. Greater radiation and correspondingly greater leaf temperatures, coupled with extreme vapor pressure deficits (VPD), suggest that on a typical sunny day the most stressed portion of the canopy was on the SW aspect during afternoons. Conversely, leaves on the NE aspect would have most suitable conditions during mornings (i.e., high PAR and low VPD) to maximize photosynthesis and water use efficiency.

Moisture Treatments

All trees received frequent precipitation during April and May, 1986, prior to initiation of the moisture treatments (fig. 3). Rain shelters were imposed May 29, about two months following budbreak of *Prosopis*, which is winter deciduous. Control and Surplus moisture trees received precipitation during June and July. Surplus trees were irrigated additionally twice in June and twice in July. Our first trial to monitor response following watering of all trees on June

28 was terminated after June 30 because a 26mm rain occurred on July 1. Sufficient time was allowed to precondition the trees prior to a second trial which began July 29. A substantial storm which even breached the rain shelters to some degree precluded a third trial scheduled for early September (fig. 3). Prior to the July 29 trial, Surplus trees received 135mm more water than Control trees in four waterings, each equivalent to 30-40mm. Rain shelters shed 110mm precipitation during that time. All trees received 40mm irrigation on July 29.

Soil Moisture

Greatest flux in soil moisture occurred in the surface 30cm and declined progressively with depth (figs. 3 and 4). Soil moisture was maintained at levels higher than the control with supplementary irrigation at most depths, but surface evapotranspiration caused moisture to decline rapidly in the 30cm depth following each irrigation (fig. 3). Major differences in soil moisture between Control and Rainout plots were not found until the 60cm depth. Increases in moisture at 30cm caused by rain were probably not detected in Control plots because we were unable to measure moisture immediately following storms due to site inaccessibility. Conversely, effects of surplus irrigation were measured immediately following watering. This artifact in sampling appeared to be restricted to the 30cm depth.

Consistent differences between all three treatments were found at 60 and 90cm depths. Differences below 90cm were minimal, indicating neither surplus nor natural moisture infiltrated below this depth. A late summer storm yielded more than 250mm precipitation, and had a measurable effect to 150cm (fig. 4).

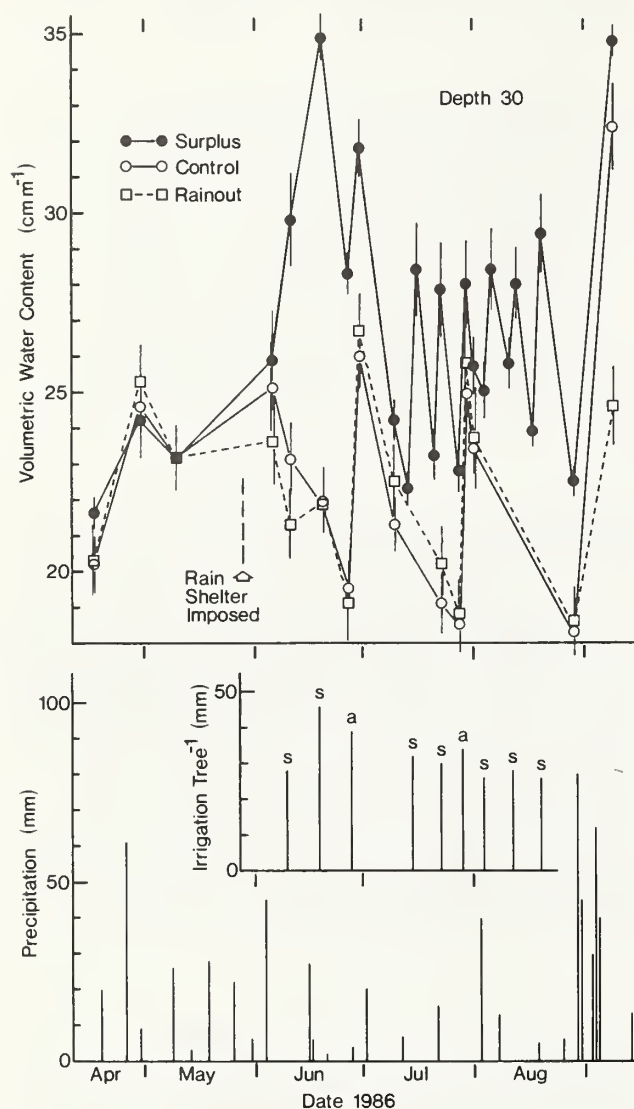


Figure 3--Soil water content at 30cm depth within root containers exposed to three moisture treatments (top), and time and amount of moisture received through natural precipitation and/or irrigation (bottom) during spring and summer 1986. Vertical dashed line indicates date rain shelters were imposed. Surplus = surplus irrigation plus natural precipitation. Control = precipitation only. Rainout = no watering except when all trees were watered June 28 and July 29. s = irrigation, surplus trees only; a = all trees irrigated. Vertical bars indicate ± 1 standard error of the mean.

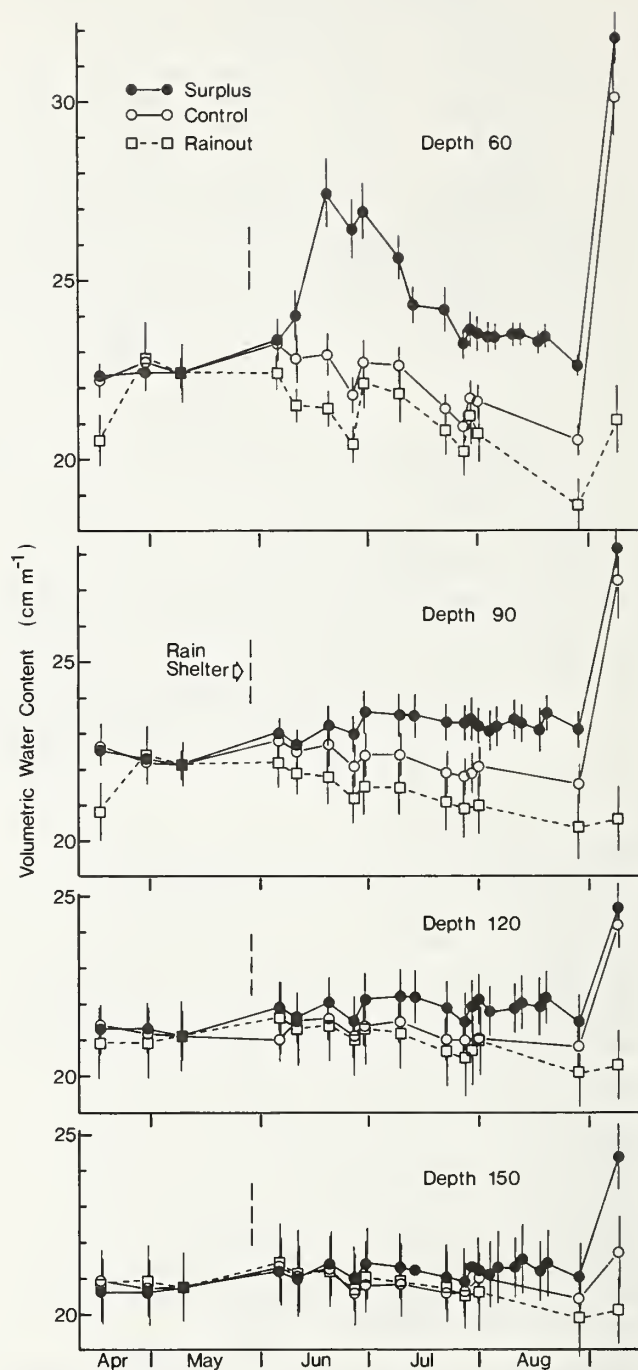


Figure 4--Soil water content at various depths within root containers of *Prosopis* trees conditioned to three different moisture treatments. Vertical dashed line indicates date in 1986 when rain shelters were imposed. Surplus = surplus irrigation plus natural precipitation. Control = precipitation only. Rainout = no watering except when all trees were watered June 28 and July 29. Vertical bars indicate ± 1 standard error of the mean.

Leaf Water Potential

Predawn leaf water potentials (WP) were significantly different between the three moisture treatments on June 27 and July 28 (fig. 5). Rain sheltered trees appeared to be under greatest stress according to predawn measurements on both dates. WP decreased in all treatments to -3 MPa by 2 HPS on both sample days and thereafter remained between -2 and -2.7 MPa (data not shown). Differences between treatments were not apparent during daylight hours on either day, indicating that for this species, predawn values offer the only valid assessment of moisture stress as it relates to leaf WP.

Effects of increasing stress from June 27 to July 28 were evident by a decline in predawn WP in all treatments to the point that Rainout trees had values below -2 MPa on July 28. Following irrigation of all trees on June 28 and July 29, differences between treatments were eliminated as WP increased to -0.9 and -1.2 MPa, respectively. Again, increasing seasonal stress caused WP to be lower following watering in July than in June. Rapid response of the trees following irrigation in the shallow root zone agrees with Sala and Lauenroth (1982) who noted the significance of small rainfall events on physiological condition of semi-arid species.

Stomatal Conductance

On both NE and SW aspects and across all treatments, stomatal conductance (CS) declined during each day, but the decline was sharper on the NE aspect following June 6 (fig. 6). These results were in response to increasing ambient temperature and decreasing RH (fig. 2).

Seasonally, while CS was generally greater across all HPS and both aspects, soil moisture was less at 30 and 60 cm depth in Surplus trees

on June 6 than on June 27 (figs. 3, 4 and 6). This finding does not support the hypothesis that *Prosopis* uses water as it is available and suggests that ambient conditions may be the most important factor which regulates CS in early summer, as shown in figure 2. These results were not seen in the Control and Rainout trees during the same interval, as CS and soil moisture both declined. From June 27 to July 28, CS declined across all treatments and HPS, except at 11 HPS when CS was nearly zero on both dates (fig. 6). These results are consistent with corresponding changes in soil moisture, WP, air temperature and RH, and support findings by others (Thomas and Sosebee 1978).

Clearer differences in CS as a result of moisture treatments were on the SW aspect on June 27 and July 28 (fig. 6). However, in spite of the fact that from May 29 to July 28 Surplus trees received 135mm more and Rainout trees received 110mm less moisture than Control trees (i.e., a moisture range of 245mm), there was surprisingly little difference in CS between treatments, especially on the NE aspect. Greater CS on the NE aspect in Surplus trees than in other treatments on June 27 and July 28 must be attributed to inherent variation among trees and not the surplus watering since these trends were apparent on June 6, prior to the first surplus irrigation. The fact that the SW aspect responded to soil moisture treatments rather than NE suggests that soil moisture content is fundamental to regulation of stomatal aperture only when ambient conditions are extreme. The tree will spend water for photosynthesis on the SW aspect in afternoons only when high available moisture conditions prevail.

Prosopis in this study appear to tolerate rather than avoid drought by maintaining high CS at low leaf WP at certain times, but not throughout the day. By adjusting magnitude of CS during the day, *Prosopis* can also be viewed as avoiding drought as outlined by Nilsen and others (1984), although this does not correspond to the classic definition of phreatophytic drought avoidance (Nilsen and others 1981). Nilsen's trees, described as phreatophytic, had access to free water at a shallow depth.

Stress History and Response to Moisture

Conductance in all trees increased across all HPS and both aspects within one day following irrigation on July 29 (fig. 7). The one day response was significantly greater than the three day response only at 8 (NE aspect) and 11 (SW aspect) HPS in Surplus trees. By contrast, greatest CS levels in the stressed trees, especially Rainout trees, did not occur until 3 days following irrigation, indicating that moisture stress retarded rapidity of response to a moisture event. The delayed response in stressed trees was more pronounced on the SW than NE aspect suggesting that recovery from stress was most difficult for leaves exposed to the most severe ambient conditions.

Across both aspects and most HPS, magnitude of response, in terms of increased CS, was greater

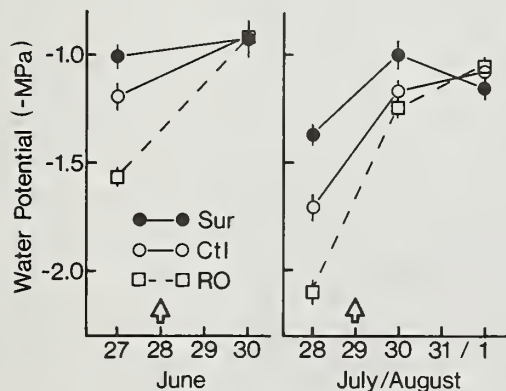


Figure 5--Predawn leaf water potentials of *Prosopis* exposed to three moisture treatments prior to and following irrigation of all trees (open arrows) on two dates in 1986. Sur = surplus + natural moisture, Ctl = control, RO = rainout treatment. Vertical bars indicate ± 1 standard error of the mean.

in Surplus trees than other trees on both sample days following irrigation (Fig. 7). An August 3 rain halted further sampling; however, rapid stomatal closure on the SW aspect experienced by the Rainout, and to a lesser degree, the Control trees, but not the Surplus trees between 5 and 8 HPS on August 1 suggests that duration of response to the irrigation was related to stress history. These results agree with the review by Kaufmann (1981) which indicated that stress history has a significant effect on stomatal behavior and hydraulic flow of water, even though leaf water potential recovers rather quickly after rewatering.

SUMMARY AND CONCLUSIONS

One of the experimental goals of this study was to observe responses of large woody plants *in situ* to moisture events, yet employ methods to control moisture availability to each plant and thereby manipulate plants of the same species to different levels of physiological condition during the same growing season. Such a design would facilitate simulation of droughts as well as wet cycles during any season. We chose to begin our studies by modifying spring and summer conditions. While results reported in this paper represent only one year of data, we feel that the

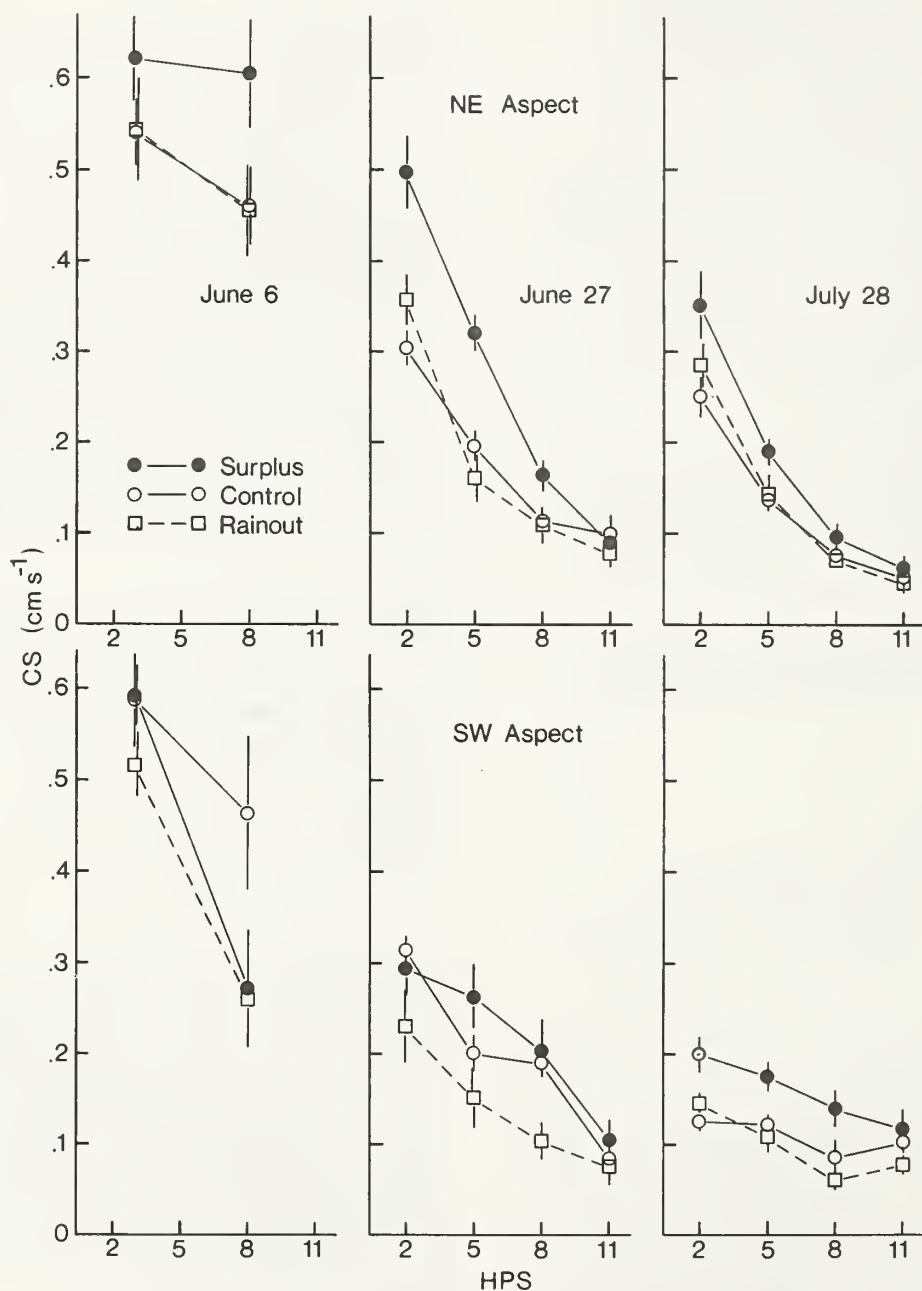


Figure 6—Diurnal stomatal conductance (CS) on northeast (NE) and southeast (SW) aspects of mesquite exposed to three moisture treatments on three dates in 1986. Vertical bars indicate ± 1 standard error of the mean.

treatment scheme we used created different moisture stress levels in *Prosopis*. Installment of the rain shelters occurred a month later than originally planned due to design problems, and we were unable to sufficiently precondition plants before late June.

The best overall indicator of moisture stress in *Prosopis* appeared to be predawn leaf water potential and not stomatal conductance, although differences in CS in response to stress treatments were measured. Stressed trees responded differently to moisture events than less stressed trees, suggesting that stress history influenced recovery from stress. Rapidity, magnitude and duration of response were slower, less, and shorter, respectively, in stressed than less stressed trees.

Water use by *Prosopis* (i.e., CS rate) was not always positively correlated with soil moisture content. As such, this study did not support a general hypothesis that *Prosopis* uses water as it is available. Ambient conditions coupled with level of plant stress influenced CS as much or more than soil moisture content during certain seasonal and/or diurnal periods.

Information from this study will be used to enhance current efforts by other research groups to model the water budget of *Prosopis*. As such, this study will augment long term efforts to increase rangeland watershed yield through proper brush control and management. This study will also aid in development of models concerning timing of herbicide application for *Prosopis* control (Dahl and Sosebee 1984). We feel there is a

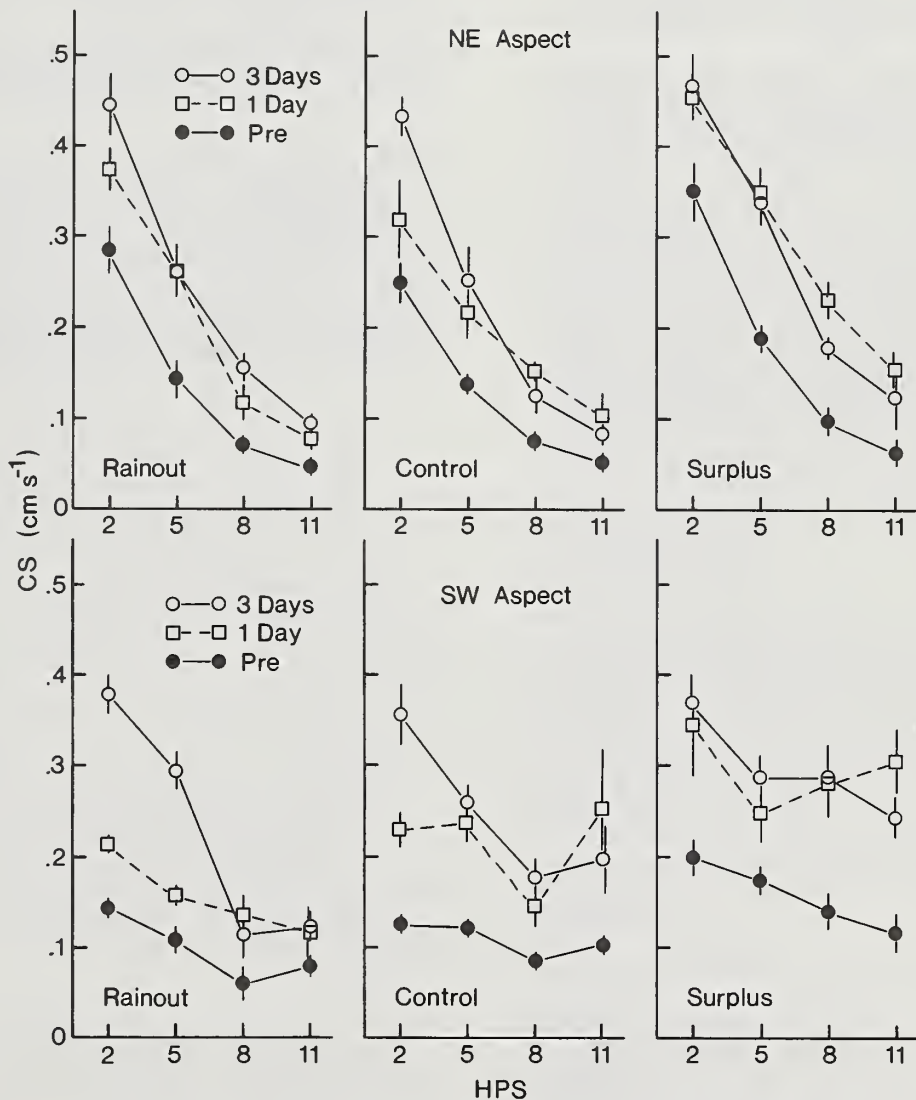


Figure 7—Diurnal stomatal conductance (CS) on the northeast (NE) and southwest (SW) aspects of mesquite trees pre-conditioned to three levels of moisture stress one day prior to (Pre) and one (1 Day) and three days (3 Days) following 40mm irrigation on July 29, 1986. Vertical bars indicate ± 1 standard error of the mean.

link between stomatal activity and efficacy of foliar applied herbicides. Information gained from this study can be incorporated into "decision aid" type models for determining date of herbicide application based on predicted conductance responses, given certain levels of plant stress and occurrence of precipitation events.

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A MODEL OF FREEZE TOLERANCE IN WINTERFAT GERMINANTS //

D. Terrance Booth

ABSTRACT: Understanding freeze tolerance mechanisms in winterfat (Eurotia lanata) seedbeds could increase the successful culture of that plant on western rangelands. Under-snow germination and tolerance of nonwoody winterfat seedlings to subfreezing temperatures has been documented by several authors; however, seedling susceptibility to freezing has also been noted and is thought to contribute significantly to seedling mortality. This paper reviews plant freeze tolerance, describes exploratory work, and presents a hypothetical model of freeze tolerance in winterfat germinants.

INTRODUCTION

Freeze tolerance by young winterfat [Eurotia¹ lanata (Pursh) Moq.; Ceratoides lanata (Pursh) J.T. Howell] plants is a documented part of the plant's seedbed ecology (Wilson 1931; Hilton 1941; Woodmansee and Potter 1971). Like several other rangeland species, winterfat is a surface germinator whose diaspores are shed in fall or winter and germinate under cool, moist conditions. Depending on the weather, young plants may exist through weeks or months of freezing temperatures as imbibed seeds, as germinated seeds (germinants), or sometimes as nonwoody seedlings. This ecological strategy allows seedling establishment and root development before the heat and drought stress of summer. It also enables the plant to compete successfully with established warm season vegetation (Woodmansee and Potter 1971). Seedbed freeze tolerance is, therefore, a major factor in seedling establishment and in plant survival.

However, winterfat seedlings can be susceptible to frost, and freezing is suspected as a major decimator of early, cotyledon-stage plants (Stevens and others 1977; Hodgkinson 1975; Stevens and Monsen 1985). The reasons for tolerance and intolerance are not known, nor have any hypotheses been advanced. This paper will review some basic facts of plant freeze tolerance

and will then consider the winterfat seedbed specifically. Exploratory work with winterfat germinants will be described and a hypothetical model of winterfat-germinant freeze tolerance will be presented.

THE PROCESSES AND PHYSIOLOGY OF FREEZE TOLERANCE

Acclimation

Acclimation and hardening are terms which describe the transition from the tender or freezing susceptible condition to the hardy, freeze tolerant condition in winter-hardy plants (Burke and others 1976). The transition occurs at the cellular level and affects membrane lipids (Yoshida 1982; Senser and Beck 1984; Lynch and Steponkus 1987), structural proteins of the membrane (Yoshida 1984), membrane enzymes (Ling-Cheng and others 1982; Hellergren and others 1983), and membrane associated cations, particularly Ca and Mg (Yoshida 1979a, 1979b, 1982; Pomeroy and Andrews 1985). These changes result in: membrane augmentation, an increased rate at which water can move through membranes (Scarth and Levitt 1937; Levitt 1978; Lyons and others 1979), cytoplasmic changes (Stout and others 1987), and changes to respiration machinery (Christiansen and St. John 1981; Cook and Cammack 1985).

Acclimation also is correlated with reduced plant-water content (Burke and others 1976). The degree of freeze tolerance is inversely related to tissue moisture in seeds (Junttila and Stushnoff 1977) and in herbaceous (Olien 1964; Metcalf and others 1970) and woody plants (Li and Wieser 1971; Levitt 1972; Olien and Smith 1981). Differences in the equilibrium moisture content appear to account for some of the differences in freeze tolerance among cereals and among seedlots of lettuce (Lactuca sativa L.) (Metcalf and others 1970; Keefe and Moore 1983).

Rates of Acclimation and Deacclimation

The time required to acclimate and to deacclimate varies by species and ranges from a few days to over 6 weeks (Olien and Smith 1981; Fennel and Li 1987). The greatest change in spinach (Spinacia oleracea L.) freeze tolerance occurred in the first 3 days of acclimation with little additional change after 14 days. Fully acclimated plants lost 3 to 5°C of freeze tolerance within 1 day. There was no further decline in tolerance after the third day of deacclimation. Wheat (Triticum aestivum L.)

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¹ Proposals for conservation of this long-used generic name have been invited (Brummitt 1978).

requires 4 to 6 weeks to fully acclimate and becomes deacclimated in about the same time period (Fennel and Li 1987).

Freezing Point Depression and Supercooling

As hardy plants are cooled below 0°C, the cells and surrounding fluid remain unfrozen due to depression of the freezing point by the solutes present and to supercooling (Lyons and others 1979). The accumulation of solutes can give freezing protection to about -4°C (Levitt 1978). This protection is important to plants with limited hardiness, to acclimating plants, and it complements other freeze-tolerance mechanisms.

Supercooling, in which liquid water remains in the plant at temperatures below the freezing point, is an important means of freezing avoidance in some woody plants (Burke and others 1976) and in some imbibed seeds (Junttila and Stushnoff 1977; Keefe and Moore 1981, 1982). However, herbaceous plants seldom supercool more than a few degrees centigrade unless tissue moisture is very low (Burke and others 1976; Ashworth and others 1985). External ice can nucleate internal supercooled water through stomates and other openings (i.e. wounds or pores) having a diameter greater than 0.01 µm (Burke and others 1976; Keefe and Moore 1982; Ashworth and others 1985). Supercooled water in woody tissue and in seeds is apparently isolated from external ice.

Supercooling is also encouraged by interaction of plant cell walls and of associated xylan mucilages with water. Fixed patterns of hydrophilic groups in substances like cellulose tend to orient molecules of a covering water film into a matching pattern. This orientation affects the freezing point of water (Olien 1965; Dennis and others 1972). Freezing is also affected by long chain polymers of mucilages which inhibit ice formation by interfering with the diffusion of water molecules to ice crystal surfaces (Olien 1965; Olien and Smith 1981; Franks 1981). The effectiveness of mucilages as cryoprotectants differ by species. The mucilages of rye (*Secale cereale* L.), for example, have been reported to be much more effective than those of barley (*Hordeum vulgare* L.) (Olien 1965).

Freeze-induced Dehydration

The freeze-dehydration process as described by Lyons and others (1979), begins at temperatures between -2 and -15 °C. The formation of ice crystals in the extracellular solution results in a disequilibrium between the chemical potential of the supercooled cytoplasm and the partially frozen extracellular fluid. Therefore moisture diffuses through the membrane to extracellular ice crystals. Cell dehydration is a function of membrane permeability and of the surface area of the plasma membrane relative to cell volume. Cell survival depends on intracellular water being removed at a rate consistent with the rate of temperature decrease. If the temperature decreases faster than the cell dehydrates,

cytoplasmic supercooling is deepened and the probability of intracellular ice increases. Intracellular ice results in death of the cell.

Intracellular ice is the primary danger to the cell; secondary threats, which may also injure or kill the cell, are mechanical injury to the plasma membrane by extracellular ice and excessive dehydration (or excessively rapid rehydration; Steponkus and Wiest 1978). The effects of dehydration can be generally grouped into three categories of "solution effects" that include physical, chemical, and electrical consequences of reduced cell moisture (Steponkus 1984).

Cooling Rate

Both minimum temperatures and the cooling rate affect plant freeze tolerance. A cooling rate of 20°C/h was found to be too rapid for freeze dehydration to occur in imbibed lettuce seeds (Keefe and Moore 1981). The seeds were killed at -14 to -18°C, whereas those cooled at 1°C/h retained their viability after exposure to -25°C (the lowest temperature tested). The cooling rates and minimum temperatures a seed or germinant is exposed to in the natural environment are modified by the earth and by insulating materials such as snow and litter cover. It is unusual for soil surfaces in mid-latitude habitats to have cooling rates faster than 5°C/h (Lowe and others 1971; Keefe and Moore 1981).

FREEZE TOLERANCE IN WINTERFAT GERMINANTS

A germinant is the stage of plant development in which the radicle, but not the cotyledons, has emerged from the bracts and pericarp. Winterfat will germinate at temperatures as low as -1°C (Stevens and others 1977; Booth 1984) and Hilton (1941) and Woodmansee and Potter (1971) have described undersnow germination that produced vigorous seedlings which appeared unharmed by -10 to -13°C temperatures.

Acclimation

Fry (1969) found that winterfat seedlings acclimated best under short-day, cold temperature conditions and that 96% of acclimated 17-day-old seedlings survived -12°C. Survival was 32% or less for older seedlings and for those not acclimated. He concluded that younger seedlings were capable of a greater degree of freeze tolerance than older seedlings. Acclimated winterfat seedlings have a relatively high 87 to 88% moisture (Booth 1987).

Protective Function of Bracts

Dispersed winterfat diaspores in contact with the earth often have a cover of other diaspores (fig. 1), of litter, or of snow which may insulate the plant from temperature extremes and from rapid rates of temperature drop. In addition, the movement of Ca and Mg from diaspore bracts into the embryo during

Table 1--Pre- and postimbibition cation concentrations in winterfat bracts and seeds¹

	Ca ⁺⁺		Mg ⁺⁺		K ⁺		Na ⁺	
	BRACTS	SEEDS	BRACTS	SEEDS	BRACTS	SEEDS	BRACTS	SEEDS
Preimbibition	13667	992	4603	1717	13187	11005	493	240
Post imbibition	13593	1627	4269	2129	6295	11465	173	134
Amount change	-74	+635	-334	+412	-6892	+460	-315	-106
² Observed F	0.01	12.06	6.25	7.71	7.71	0.29	3.85	5.62
³ O.S.L.	NS	0.05	0.10	0.05	0.05	NS	NS	0.10

¹ Data are from Booth 1987. Values are mean of 3 replications.

² Testing the null hypothesis that postimbibition concentrations are not different from preimbibition concentrations.

³ Observed significance level.



Figure 1--An aggregation of winterfat diaspores, litter and seedlings illustrating the protecting influence of covering material.

imbibition (table 1) may increase freeze tolerance. Schmidt and others (1986) have found that salt treatment of hydroponically grown spinach hardened the leaves against mechanical damage of freezing. Salts from winterfat bracts may provide similar protection to winterfat germinants.

Supercooling and Freeze Dessication: A Test of Mechanisms

Introduction--Hilton (1941) reported vigorous growth from winterfat seedlings which were "frozen solid 16 hours of 24." However, he provided no evidence of ice crystals in plant tissues and his comment may have referred to the minimum temperature (-4°C) in his germinator. That temperature is within the range that plants tolerate cold by freezing avoidance; that is by freezing point depression and by supercooling.

To determine whether winterfat germinants supercool or freeze-dehydrate under nonlethal freezing, the conductivity methods of Olien (1961, 1964; Dennis and others 1972) were adapted to study freezing patterns in winterfat germinants. This entails measuring the conductivity of the plant's extracellular solution as the temperature is reduced. Olien (1964) has shown that as extracellular solutions freeze, the conductivity decreases; and, he has described equilibrium and nonequilibrium conductivity-freezing patterns in tolerant and

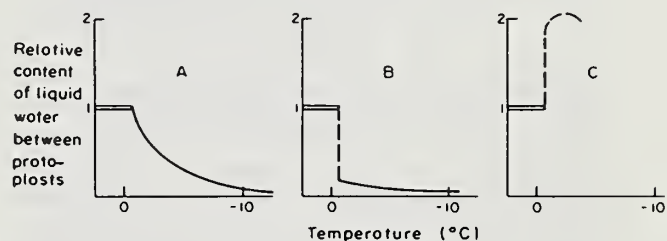


Figure 2--Three principal types of freezing patterns found in different tissues of the barley crown (Olien 1964); (A) Equilibrium freezing pattern, (B) Non-equilibrium freezing pattern, (C) Non-equilibrium freezing pattern typical of tender tissues.

intolerant plant tissue (fig. 2). An equilibrium freezing pattern is typical of acclimated tissue in which the extracellular moisture is closely associated with the cells, the equilibrium of water distribution shifts smoothly and the conductivity-freezing pattern is temperature controlled. The non-equilibrium patterns are not temperature controlled and are evidence of freezing injury to tissues. Figure 2-B shows sudden readjustment of extracellular liquid water. This type of freezing produces large, injury causing, ice crystals. Figure 2-C indicates rupture of protoplasts with freezing.

Methods--To study freezing patterns in winterfat germinants, diaspores were soaked for 2 days at $0 \pm 2^\circ\text{C}$, allowed to germinate at temperatures between 0 and 5°C , then held at 0°C until used 7 to 14 days after being soaked. For each test the bracts and pericarp were removed from the cotyledons and the plant then bedded in dry graphite within the head-slots of two brass screws as shown in figure 3. Plants were sealed into the slot with a 1:10 wet paste of graphite and agar. When the paste dried, the screw heads (electrical contacts) were covered with silicone grease to prevent current being conducted in moisture that might occur on the outside of the plant. The test plant and contacts were then covered with a sheet of laboratory film and the apparatus connected to a YSI Model 32 conductivity meter with 0.4 mm diameter copper wire. The range of the conductivity meter was set on 2 μmhos and a strip chart recorder

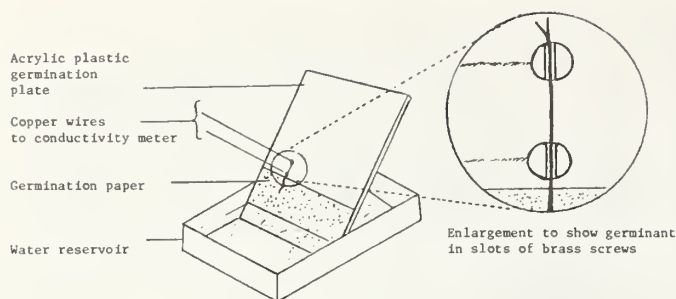


Figure 3--Illustration of experimental apparatus.

connected to the conductivity meter. The recorder span was 100 mV/FS and the chart rate was 0.25 cm/min. Plants were placed in the growth chamber and the system was allowed to equilibrate at 10°C for 1/2 h. The growth-chamber temperature was then dropped to -5°C at 7.5°C/h. A -5°C temperature was maintained for 1 h, after which the temperature was reduced to -20°C at an average rate of 5°C/h, reset to -5°C for 1 h then raised to 0°C. Minimum temperature was checked with a minimum/maximum mercury thermometer placed in the germinator adjacent to the test apparatus. The test plants were cultured at nonfreezing temperatures for several days after the test, to check viability.

Results and Discussion--During the tests conductance remained constant to -8°C to -11°C, then decreased as the temperature decreased. The conductance pattern (fig. 4) was similar to that described by Olien (1964) as an equilibrium freezing pattern, but occurred at lower temperatures than he has illustrated for barley crown tissues. The thawed germinants had no visible signs of damage though subsequent growth at warm temperatures was slow.

The tests indicate:

- (1) that germinants can supercool to -8°C or lower. The capability to supercool 8 to 10°C may be a buffer against rapid cooling and would be a distinct advantage for high moisture plants germinating on the soil surface in harsh climates.
- (2) that germinants can tolerate the formation of ice crystals in plant tissues and do freeze-dehydrate.
- (3) that acclimated germinants can survive temperatures at least as low as -20°C.

There are some questions. These data contrast with observations that herbaceous plants seldom supercool more than a few degrees unless tissue moisture is very low (Burke and others 1976; Ashworth and others 1985). Keefe and Moore (1981) have shown that imbibed lettuce seeds will supercool to -16°C. However, this happens only if the endosperm, which acts as a nucleation barrier, is intact. There is no nucleation barrier in winterfat germinants. Further, the cellulose materials surrounding the test plants, or other conditions of test, may have allowed germinants to supercool to a degree that would not occur in the natural environment

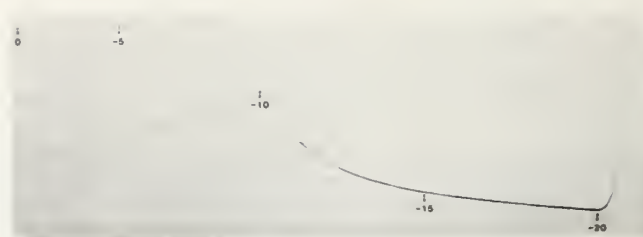


Figure 4--Strip-chart recorder output showing conductivity-freezing pattern of winterfat germinant. The recorder span was 100 mV/FS and the chart speed was 0.25 cm/m.

(Olien 1965). Finally, the conductivity data are only an indication of supercooling and not direct evidence.

If germinants do naturally supercool, that capability must depend on the small size of the plant (Ashworth and others 1985), on interaction of water with plant cell walls and mucilages, and on lack of development of the vascular cylinder (Olien 1964; Dennis and others 1972). Vascular cylinder development increases the quantity of water in the conducting vessels and reduces intimate association of water molecules with living cells. Both factors increase the probability of ice nucleation.

Observations of fresh cross-sections of winterfat germinants and nonwoody seedlings under the microscope support the above observations. They also suggest an explanation for Fry's (1969) finding of decreased freeze tolerance with increased development of nonwoody seedlings. Cross-sections were obtained by placing germinants or young seedlings in water to which a few drops of safranin stain had been added. After 15-30 min. plants were sectioned at the point where the stem and root join, and the tissue examined and photographed under 100 and 250 magnification. Photomicrographs (fig. 5) of the same group of plants as germinants and 8 days later (4 days of which included 16 h/d at 20°C), as seedlings, show the older plants have root hairs, xylem vessels and large diameter cells not seen in the younger, less developed plants. The probable result of vessel development on freeze tolerance was discussed above. The larger cells may also reduce freeze tolerance. As a cell grows the surface area of the plasma membrane increases by the square, but the volume of the cell increases cubically. If the permeability of the plasma membrane remains constant, the larger cell has relatively less capacity to dehydrate and is more at risk as the temperature decreases.

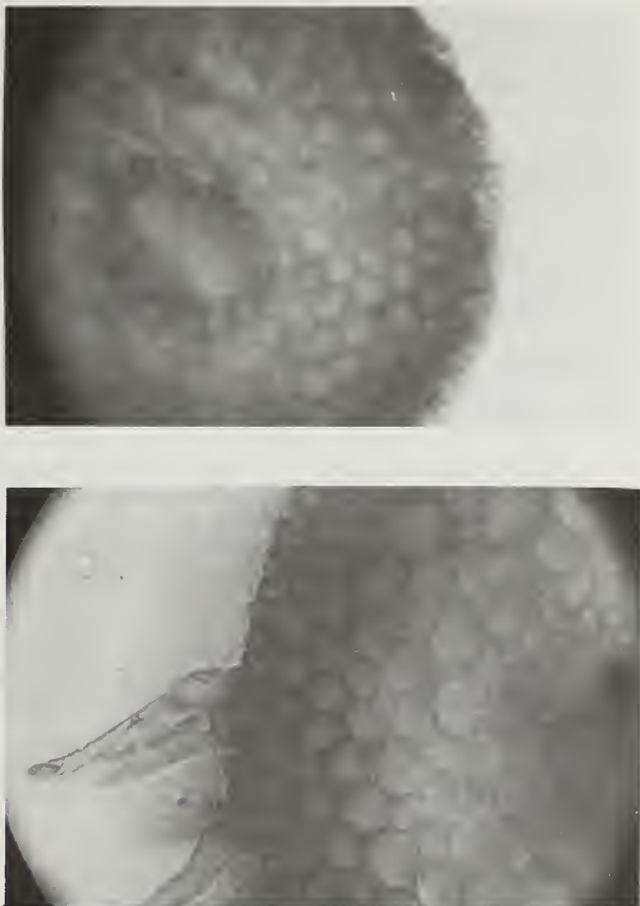


Figure 5--Fresh cross-sections of winterfat germinant (top) and seedling (bottom). x 100.

SUMMARY

The winterfat germinant's first defense against cold is the earth and the insulating influence of diaspore bracts, litter and snow. The second defense appears to be the capability to supercool at high moisture levels. That tentative capability, if it exists, is likely to be a function of plant size, immature cells and of an undeveloped vascular cylinder. Thirdly, winterfat germinants appear to undergo freeze dehydration, a process which may allow the plants to tolerate temperatures even lower than -20°C .

The literature reviewed and the exploratory work described have defined some important research questions relating to cold tolerance in nonwoody winterfat plants. As these questions are resolved and as our understanding of seedbed freeze tolerance is improved, our capability to successfully culture winterfat and other rangeland plants will be extended.

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WATER RELATIONS, ABOVEGROUND GROWTH, AND PHENOLOGY OF ARTEMISIA TRIDENTATA SPP. VASEYANA
IN RELATION TO DISPERSION PATTERN //

Alan T. Carpenter and Neil E. West

ABSTRACT: Water relations, growth, and phenology of Artemisia tridentata ssp. vaseyana (mountain big sagebrush) were investigated in a field experiment in southwestern Wyoming. Artemisia transplants were grown in plots where the individuals were either regularly dispersed or clumped. Overall, plants in the regularly dispersed treatments appeared to have a growth advantage compared to clumped plants. This probably reflected greater use of soil water by the regularly dispersed plants and more deposition of blowing snow among the regularly dispersed shrubs.

INTRODUCTION

Shrubs in arid environments commonly grow in clumps (MacMahon and Schimpf 1981; West 1987). This could arise from limited seed dispersal ability, causing recruitment to be concentrated near the maternal parent plants (Friedman and Orshan 1975). Alternatively, the clumps could develop in microsites where resources such as water and nutrients are concentrated (Waisel 1971; Barbour and others 1977). It is also possible that clumps of shrubs could improve their local environmental conditions by trapping blowing snow and airborne particulates, and by serving as foci for animal activity (West 1987).

If clumps of shrubs develop largely from limited seed dispersal, the clumps should be transient, with dispersion changing to a more random or even regular pattern over time. Closely spaced plants would succumb from the effects of competition more rapidly than shrubs spaced farther apart. Efforts to detect changes in pattern with increasing shrub size or age or on low precipitation sites have produced mixed results (for example, Beals 1968; Anderson and others 1969; Woodell and others 1969; Barbour and Diaz 1973; Malik and others 1976; Williams and others 1978; Phillips and MacMahon 1981; West and Goodall 1986). Perhaps, this is not surprising in view of the usual lack of control over local variations in soil moisture (Greig-Smith and Chadwick 1965).

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The results of manipulative experiments indicate that plants in hot deserts can compete with their neighbors for water. Fonteyn and Mahall (1978, 1981) found in their removal experiments in the Mojave Desert of California, that plants that had their neighbors removed had more positive xylem water potentials than control plants. Robberecht and others (1983), also using removal experiments in the Mojave Desert, found that Hilaria rigida individuals with their nonspecific neighbors removed had more positive leaf water potentials plus greater leaf conductances, and greater above- and belowground biomass production than control individuals. Ehleringer (1984) removed the neighbors from Encelia farinosa individuals in the Sonoran Desert of Arizona and found that these Encelia plants responded with improved water relations, growth, and reproduction relative to control individuals.

It is unclear if the above results apply to cool semi-deserts, such as the Great Basin. Here, annual precipitation is typically greater, and potential evapotranspiration is lower than in the Mojave or Sonoran Deserts. Most precipitation in the Great Basin falls as snow, which is considerably redistributed by prevailing winds and, at least in some locations, tends to accumulate around shrubs. In this region, clusters of shrubs may result from a combination of topographic position and moisture accumulation with shrubs themselves causing substantial amounts of snow to accumulate (Allen and others 1987).

METHODS

Study Site and Experimental Design

The study site was located at the Pittsburgh & Midway Coal Mining Company's coal strip mine near Kemmerer in southwestern Wyoming. The site was stripmined in the late 1970's, later backfilled and regraded. The original topsoil, which had been stockpiled nearby, was reapplied to a depth of 10-20 cm in August 1981. It is likely that disturbance of the site during topsoil removal, stockpiling, and reapplication greatly reduced spatial variation in soil properties such as nutrient content and texture. Islands of fertility (Garcia-Moya and McKell 1970; Charley and West 1975) which may have existed on the site prior to mining, were eliminated; thus, the experimental shrubs initially experienced a relatively uniform soil environment.

The site elevation was 2,210 m and the mean annual precipitation from 1951 through 1980 at the town of Kemmerer, about 15 km east of the study site, was about 230 mm, about half of which fell as snow (National Oceanic and Atmospheric Administration 1982). The experimental plots were located on a gentle east-facing slope.

The local vegetation is included in the western Intermountain sagebrush steppe type (West 1983) with woody *Artemisia* species as the dominant plants. Winters are long and severe. The growing season for *A. tridentata* ssp. *vaseyana* in this locale lasts from late May to mid-August.

Artemisia tridentata ssp. *vaseyana* (mountain big sagebrush) was selected as the experimental shrub. It is abundant locally and dominates 10 million hectares of U.S. rangeland (Beetle 1960). On the basis of biweekly observations of snow accumulation during the winter of 1981-82, shrub clumps were seen to collect substantial amounts of snow.

One-year-old mountain big sagebrush transplants were planted in May, 1982, either individually (clumps of 1) or in clumps of four. There were three blocks each of the clump-1 and clump-4 plots. Within each clump-1 plot, 49 individuals were situated in a grid pattern with an interplant distance of 1.3 m along the main grid axis. Within each clump-4 plot, the distance between plants within a clump was 0.4 m, and the clumps were 2.6 m apart center to center (fig. 1). The overall density in the clump-1 and clump-4 plots was the same, namely 0.6 plants m^{-2} .

Because of their great size range, seedlings were separated into groups of large, medium, and small plants prior to transplanting. Plant material for each treatment was randomly drawn from each of the three groups for the three blocks, respectively. Thus, the experiment was blocked by initial plant size. Hereafter, small-, medium-, and large-plant blocks refer to the blocks consisting initially of the small, medium, and large plants, respectively. The plots were randomly assigned to positions in a long, rectangular strip of land. The randomization resulted in complete segregation of the treatment blocks (fig. 1). Hurlbert (1984) argued that such designs lack interspersions and should not be subjected to inferential statistical analysis. We have followed his suggestion.

Data were collected on the interior plants and the average computed for each block. All of the plots were weeded regularly to eliminate potentially confounding effects of differential weed density. During 1983 and 1984, meteorological data were collected at a weather station located about 300 m from the study site.

Soil and Plant Water Potential

During the summers of 1983 and 1984, soil water potential at 20- and 50-cm depths under four plants in each plot was determined using soil thermocouple psychrometers installed in 1982.

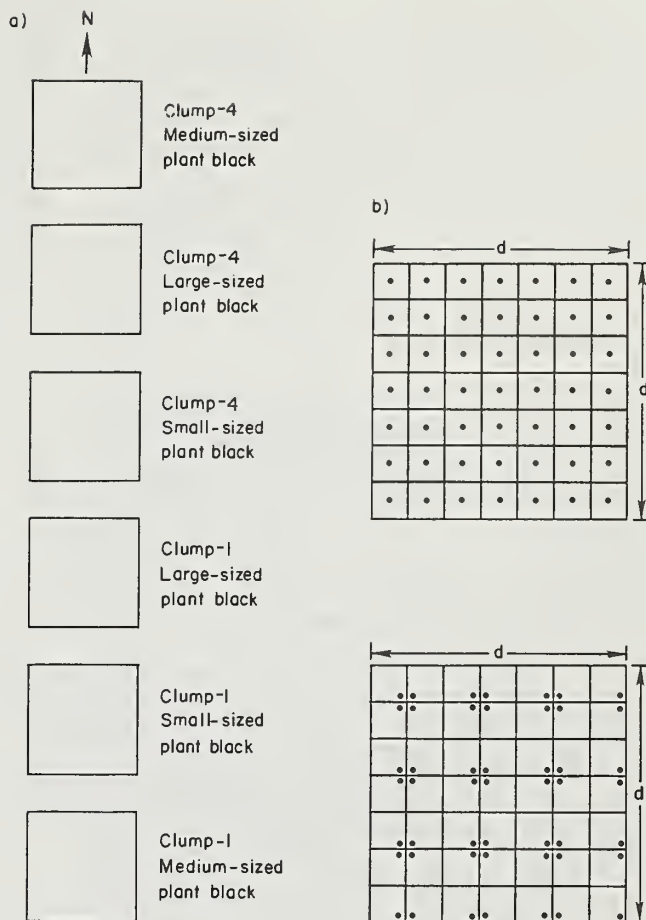


Figure 1.-- Schematic for clump-1 and clump-4 plots. (a) Plot layout in the field showing lack of interspersions; (b) dispersion patterns used in clump-1 (top) and clump-4 (bottom) plots. "Cell" dimensions are 1.3 by 1.3 m. Plant spacing within clumps of 4 = 0.4 m. Each "." denotes one shrub.

Also, two pairs of psychrometers were installed at the same soil depths between adjacent plants (clump-1) or between adjacent clumps (clump-4) in each plot. Measurements were made at dawn. Water potentials were calculated using a computer program that compensates for variable psychrometer correction coefficients, zero offsets, and soil temperatures (Brown and Bartos 1982).

In 1984, predawn and midday leaf water potentials were measured using leaf thermocouple psychrometers. From four to six ephemeral leaves were plucked from the top of each sample plant canopy ($n=6$ per plot) then quickly sealed inside a leaf psychrometer chamber. After a 2-hr equilibration period in an insulated water bath, the microvolt output of each psychrometer was recorded. The psychrometers were then frozen in liquid nitrogen, thawed in a bucket of water, and placed in the water bath for another 2 hr. The microvolt output of each psychrometer was again recorded. Total water potential and osmotic

potential were calculated using data from fresh and thawed leaf samples, respectively. The osmotic potentials were corrected for dilution of the symplastic water by apoplastic water by dividing each osmotic potential by 0.90, the average symplastic water fraction, which was obtained from pressure-volume curves. The difference between a sample's total water potential and corrected osmotic potential was considered to be a measure of leaf turgor potential.

Aboveground Phytomass

About a month after outplanting, the total aboveground mass of each of the big sagebrush transplants was estimated using the reference unit method (Andrew and others 1979, 1981; Carpenter and West 1987). This procedure was repeated at the end of the 1982, 1983, and 1984 growing seasons. The phytomass estimates were transformed to natural logarithms and the average relative growth rates for the three growing seasons were calculated (Hunt 1978).

The use of average relative growth rate permits valid comparisons even though the initial mean phytomass values were unequal, thus eliminating any possible bias created by the existence of the larger plants in the large plant block of the clump-1 treatment. During this first year the initial phytomass estimates were made on June 17, therefore, the phytomass estimates for 1982 reflect growth over only part of the growing season. The average relative growth rates for the first year are not comparable to the average relative growth rates for the subsequent two seasons.

Twig Phenology

During the 1983 and 1984 growing seasons, twig phenologies were sampled on 16 plants in each of the experimental plots. Three twigs were selected in a stratified random manner, one twig located on the east, west, and south side of each plant. The selected twigs were tagged with 2-cm length of different colored insulated wire so each twig could be followed over the growing season. At approximately weekly intervals, twig phenology was assessed on the same twigs using a scale modified from DePuit and Caldwell (1973).

RESULTS

Soil and Plant Water Potential

Differences between the clump-1 and clump-4 soil water potential means under plants both at the 20- and 50-cm depths were generally small during 1983 (fig. 2b). There was no clear tendency for the clump-1 means to be more negative or positive than the clump-4 means. On most sampling dates, the soil water potential means at 50 cm were greater than those at 20 cm, regardless of clump type. Mean values of soil water potential under plants

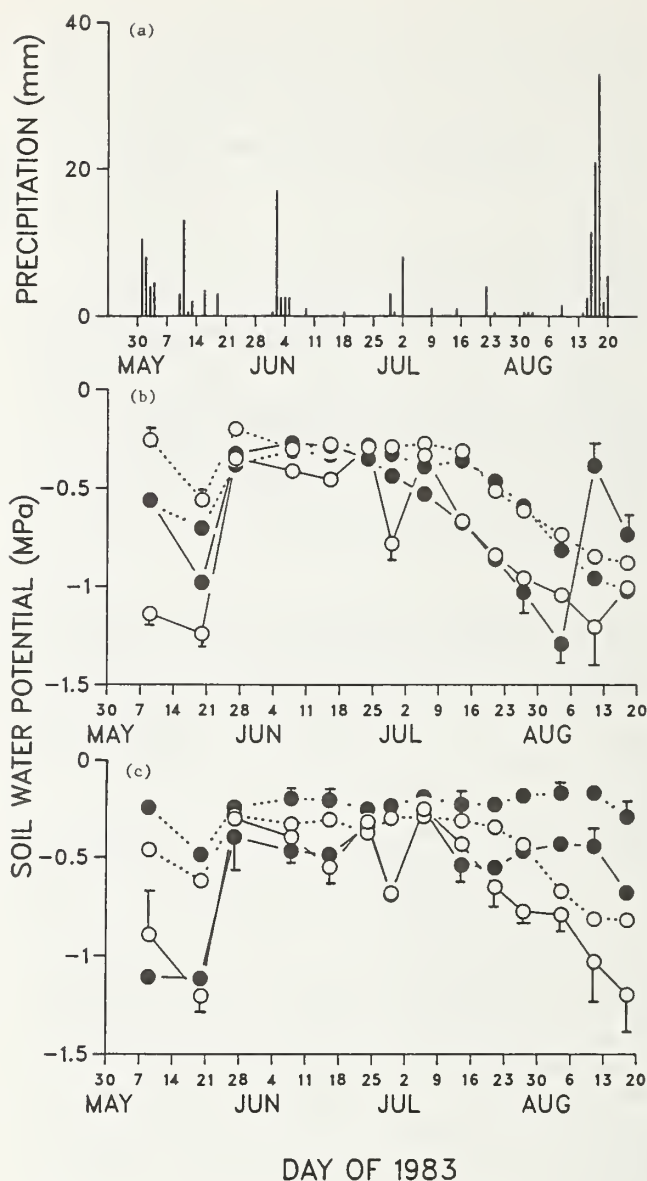


Figure 2.-- Precipitation and soil water potential in clump-1 and clump-4 plots during May-August 1983. (a) Precipitation at study site; soil water potential, (b) under plants, and (c) in interspaces between plants. Open symbols denote clump-1 means, and closed symbols denote clump-4 means. Solid lines connect 20-cm-depth means, and dotted lines connect 50-cm depth means. Vertical bars equal 1 S.E.M.; n=3.

never dropped below -1.22 MPa, and for much of the season were greater than -1.0 MPa.

Soil water potentials in the interspaces of the clump-1 and clump-4 plots during 1983 were very similar to those under plants at both the 20- and 50-cm soil depths until early July (fig. 2c). Thereafter, the soil water potentials in the clump-4 plots decreased only slightly while those in the clump-1 plots decreased more precipitously.

During 1984, soil water potential under plants in the clump-1 plots generally equaled or exceeded that in the clump-4 plots at 20 cm while the reverse was true at 50 cm (fig. 3b). Soil water potential at 20 cm was less than that at 50 cm in both the clump-1 and clump-4 plots.

Soil water potential in the interspaces between plants in the clump-1 plots was nearly always lower than in the clump-4 plots (fig. 3c). During July and August, the difference between clump-1 and clump-4 soil water potential increased at both soil depths.

Both predawn and midday leaf water potentials during 1984 in clump-1 plots were slightly higher than in clump-4 plots (fig. 4a). Leaf water potential usually dropped from predawn to midday for both clump types, increasingly so until late July. Clump-1 plots did not exhibit consistently lower or higher daily change in leaf water potential than clump-4 plots.

Leaf osmotic potentials of clump-1 plants were consistently greater than those of clump-4 plants after June 11 (fig. 4b). There was no consistent difference in daily decline in osmotic potential or in predawn or midday turgor potential between the clump-1 and clump-4 plots. There was no evident trend for daily decline in leaf turgidity to increase seasonally (fig. 4c).

Aboveground Phytomass

At the end of the 1982, 1983, and 1984 growing seasons, the mean phytomass for the clump-1 plots consistently exceeded the mean for the clump-4 plots (table 1). However, this occurred because

Table 1.--Initial and end-of-season aboveground phytomass of individual plants in clump-1, clump-4 plots for 1982-84. Means (g) \pm 1 S.E.M., n=3

	Initial	End-of-Season		
	1982	1982	1983	1984
Clump-1	2 \pm 1	7 \pm 3	100 \pm 30	230 \pm 80
Clump-4	1 \pm 0	5 \pm 1	80 \pm 4	180 \pm 20

the initial mean for the clump-1, large-plant block was 50 percent larger than the corresponding initial clump-4 plot mean.

The average relative growth rates were very similar for the clump-1 and clump-4 plots for all 3 years (table 2). Relative growth rate declined markedly from the 1983 to 1984 growing seasons.

The clump types were not very different in their phenological progression from dormant buds to rapidly elongating vegetative twigs to initiation of floral buds (table 3). As the 1983 season

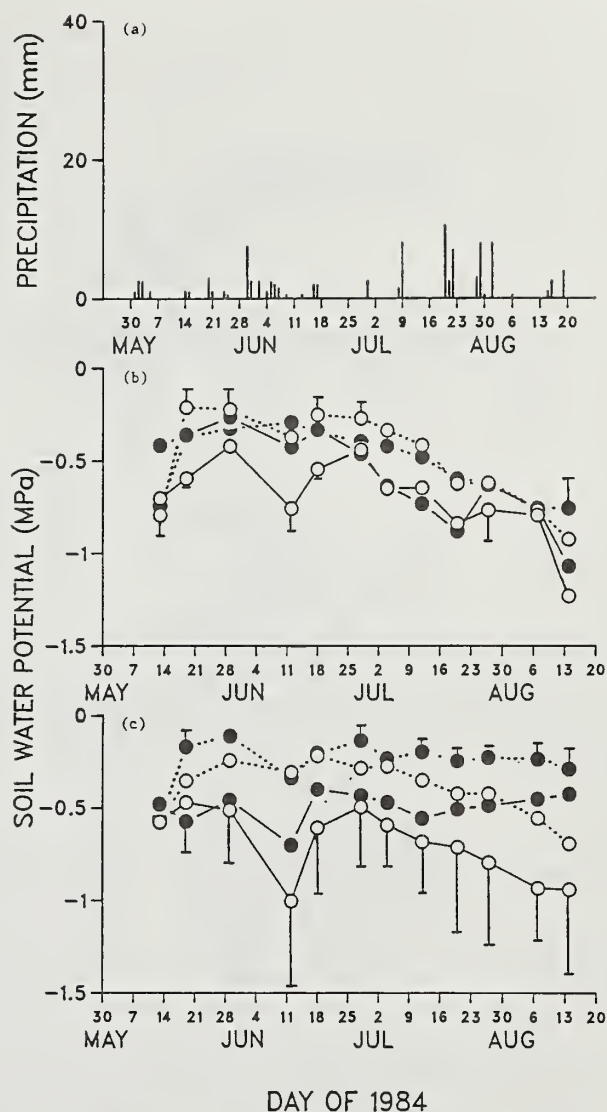


Figure 3--Precipitation and soil water potential in clump-1 and clump-4 plots during May-August 1984. (a) Precipitation and study site; soil water potential, (b) under plants and, (c) in interspaces between plants. Open symbols denote clump-1 means, and closed symbols denote clump-4 means. Solid lines connect 20-cm-depth means, and dotted lines connect 50-cm-depth means. Vertical bars equal 1 S.E.M., n=3.

Table 2--Average relative growth rate of individual plants in clump-1 and clump-4 plots for 1982-84. Means (year⁻¹) \pm 1 S.E.M., n=3. For additional details regarding units, see text

	Beginning of 1982 growing season--end of 1982 grow season	End of 1982 growing season--end of 1983 grow season	End of 1983 growing season--end of 1984 grow season
Clump-1	1 \pm 0	3 \pm 0	1 \pm 0
Clump-4	1 \pm 0	3 \pm 0	1 \pm 0

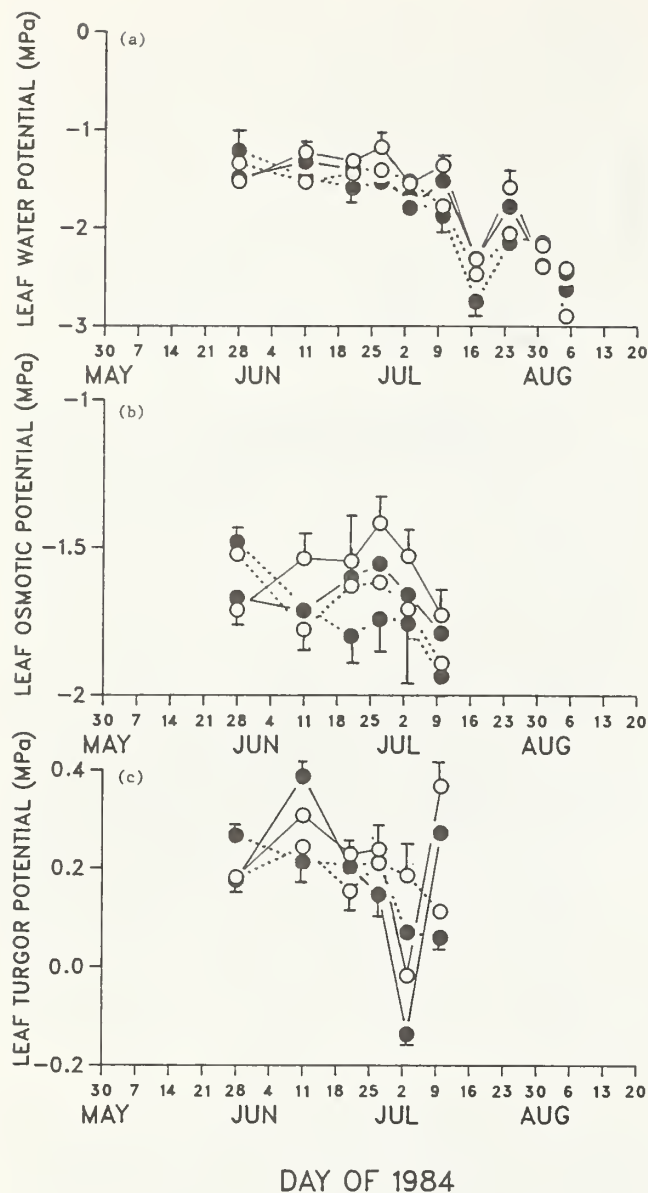


Figure 4--Water potential components in clump-1 and clump-4 plots during May-August 1984. (a) Total, (b) osmotic and, (c) turgor potential. Open symbols denote clump-1 means, and closed symbols denote clump-4 means. Solid lines connect predawn means, and dotted lines connect midday means. Vertical bars equal 1 S.F.M., $n=3$.

progressed, the proportions of twigs in the first three categories were fairly similar for the clump-1 and clump-4 plots. However, the clump-1 plots consistently had about twice as many twigs with floral buds developing as did the clump-4 plots. In 1984, the proportions of twigs in the various phenological stages were similar on each sampling date (data not shown).

DISCUSSION

There were few differences in soil water potential directly under the shrubs attributable to clump type. Soil water potential appeared to be much more affected by depth of measurement and the presence or absence of recent precipitation. However, differences in soil water potential between plants in the clump-1 and clump-4 plots did develop in the latter half of the 1983 and 1984 growing seasons. Soil water potentials at 20 and 50 cm were similar under plants and in the interspaces between plants in the clump-1 plots (figs. 2 and 3). This contrasts with the clump-4 plots where soil water potentials at both depths were higher in the shrub interspaces. Clump-4 plant roots may have extracted less soil water than the clump-1 plants. Thus, considerable soil moisture between the clumps of four plants may have gone unutilized by the shrubs both years. This is consistent with our observations that recruitment and initial growth of weeds was greater in the clump-4 plots compared to the clump-1 plots.

During the latter half of the 1984 growing season, differences in soil water potential among the large-, medium-, and small-plant blocks developed. At 50 cm, both under plants and in the interspaces between plants, the large-plant blocks had the lowest soil water potential while the small-plant blocks had the highest. In addition, differences between treatments were greater for the large-plant blocks than for the other blocks. Thus, the treatments may have had an influence only with the large-plant blocks. The shrubs may have had to attain some minimum size before dispersion pattern had any effect on soil water potential.

Mountain big sagebrush roots within the perimeter of the clumps of four plants may have overlapped greatly. However, the plants did not fully compensate by extending root growth laterally into soil with high water potential. Rodriguez (1985) found that mountain big sagebrush individuals planted in the vicinity of our plots exhibited little lateral root growth, with most roots located within 30 cm of the plant center. In September 1984, we excavated two isolated sagebrush shrubs that had been planted at the same time as the experimental plots. Soil was removed in 20-cm layers to a depth of 60 cm and outward to 1 m in one quadrant adjacent to each shrub. Visible roots were concentrated under each canopy, although an occasional root extended farther from the shrubs. Vertically, roots appeared to be most abundant from 0-30 cm in the soil. Tabler (1964) and Sturges (1977) found that mountain big sagebrush roots were concentrated close to the plants, although the maximum lateral spread was about 1.5 m. Root competition for soil water within the clumps may have reduced or eliminated any benefit those plants might have derived from snow trapping.

Table 3.--Phenological stage of tagged twigs in clump-1 and clump-4 plots in 1983. Percentages of twigs in each phenological stage. Phenological stage 2 = overwintering buds not elongating; 3 = twigs rapidly elongating in vegetative phase; 4 = floral buds developing

Phenol. stage	6 June		14 June		23 June		29 June	
	Clump-1	Clump-4	Clump-1	Clump-4	Clump-1	Clump-4	Clump-1	Clump-4
Dead	0	0	0	1	0	1	0	1
2	34	41	25	26	22	24	19	23
3	66	59	75	73	78	75	81	76
4	0	0	0	0	0	0	0	0
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Phenol. stage	6 July		13 July		21 July		27 July	
	Clump-1	Clump-4	Clump-1	Clump-4	Clump-1	Clump-4	Clump-1	Clump-4
Dead	0	1	3	1	4	4	6	9
2	16	22	13	22	13	19	11	16
3	75	72	62	67	54	60	50	61
4	9	5	22	10	29	16	33	15
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Phenol. stage	4 August		11 August		21 August			
	Clump-1	Clump-4	Clump-1	Clump-4	Clump-1	Clump-4	Clump-1	Clump-4
Dead	10	12	12	16	13	18		
2	9	13	8	12	7	11		
3	47	57	46	53	46	52		
4	34	18	34	18	34	18		

Soil water potential declined together with leaf water potential over the summer of 1984, but there was no indication that clump-1 plants behaved differently than clump-4 plants (fig. 5). Shrubs in the large-plant blocks reduced soil water potential to a minimum of -1.2 MPa while shrubs in the other blocks reduced soil water potential to 0.6 MPa. Also, the decline in leaf water potential per unit decline in soil water potential at 50 cm was lower in the large-plant blocks. These observations may have resulted from higher rooting density at 50 cm under the larger shrubs, causing daily equilibrium between plant and soil at dawn to become more fully established. The considerable scatter in the data contrasts with the results of Sala and others (1981) who found a very close relationship between water potential in the wettest soil layer and predawn leaf water potential. Perhaps, the 50-cm depth at which we measured soil water potential was not always the wettest part of the soil profile. Branson and others (1976) found that plant water potential in big sagebrush was highly correlated with minimum soil water potential, but under moist conditions factors other than soil moisture appeared to exert control over plant water potential.

If differences in soil-plant water relations were to materialize, they would have little effect on production if the differences did not substantially affect net carbon assimilation of big sagebrush. DePuit and Caldwell (1973, 1975) found that net photosynthesis in big sagebrush was strongly affected by plant water potential. They found that net photosynthesis was much greater for plants in the "emergent new leaves" and "rapid vegetative growth" phenological stages than for the later stages of "reduced vegetative growth" and "reproductive shoots full size." Thus, if major differences in leaf water potential developed between clump-1 and clump-4 big sagebrush plants only after they had passed

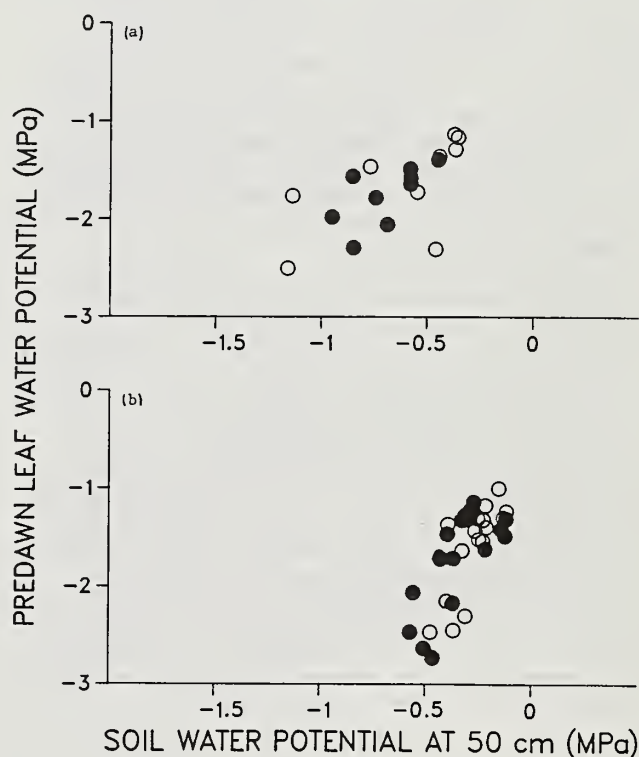


Figure 5-- Soil-plant water relationship for clump-1 and clump-4 plots under plants during May-August 1984. (a) Large-plant blocks, and (b) medium- and small-plant blocks. Clump-1 data are denoted by open symbols; clump-4 data are denoted by closed symbols.

through the rapid vegetative growth phenological stage, little difference in seasonal production between the clump types should occur.

We attribute part of the lack of observed effects of clump type on soil or leaf water potential to the abundant precipitation during 1981-1984. Three successive wet years probably meant that the soil profile was completely saturated to the maximum rooting depth of the big sagebrush plants at the beginning of the 1983 and 1984 growing seasons. In addition, the elimination of weeds in the plots meant that some soil water which would have been transpired by the weeds was available to the big sagebrush plants.

During the summer of 1983, the longest "dry" period lasted from June 5 to August 16, although numerous small rain showers, including an 8-mm event on July 2, occurred in that interval. During the summer of 1984, the longest "dry" period ran from June 7 to July 20, including an 8-mm event on July 9. Perhaps, it is not surprising that major differences in soil and leaf water potentials between clump types failed to appear.

An additional factor that may have eliminated treatment effects relates to the increase in shrub size during the study. As the shrubs grew from 1982-84, the scale of snow trapping behavior may have changed. Tabler and Schmidt (1985) proposed that snow deposition around shrubs follows the relationship: $S = H - 0.01 A D^{-1}$. Here, S = snow depth, H = height of shrub above the ground, A = shrub surface area normal to the prevailing wind, and D = shrub width or diameter. When the shrubs were small, canopies did not overlap even in the clumps of four. If plants in the clump-1 and clump-4 plots had about the same average heights and widths, the amount of snow trapped should have been about the same.

However, by the end of 1983, each clump-1 plot could be regarded as a large cluster. Shrub canopies in the clump-1 plots did not overlap, and shrub density was nearly optimal for snow trapping (Tabler and Schmidt 1985). On the other hand, plants in the clump-4 plots had dense, intermingled canopies. These clumps could be regarded as large single plants in terms of their snow trapping ability, but the clumps were not as wide as the summed widths of four single shrubs. Tabler and Schmidt (1985) also noted that dense canopies, as in the clumps of four, are less efficient snow trappers than more diffuse canopies, as in the clump-1 plants. These factors could have reduced snow trapping in the clump-4 plots compared to the clump-1 plots in the winter of 1983-84.

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245 STOMATAL SENSITIVITY AND WATER-USE EFFICIENCY IN OAKS AND THEIR HYBRIDS //

James R. Ehleringer and Mark P. Smedley

ABSTRACT: The sensitivities of stomata to changes in the leaf to air water vapor gradient (Δw) were measured on oaks (*Quercus gambelii*, *Q. macrocarpa*, and *Q. turbinella*) and their hybrids growing under common field conditions in the Cottam Oak Hybrid Grove at the University of Utah. The ranking order for decreasing sensitivity of leaf gas exchange to changes in Δw was *Q. turbinella*, *Q. gambelii*, and *Q. macrocarpa*. In addition, leaf carbon isotope ratios, an indicator of long-term water-use efficiency, were measured on these same plants. These data suggest that leaf water-use efficiencies are lowest in *Q. gambelii* and higher in both *Q. macrocarpa* and *Q. turbinella*.

STOMATA AND HUMIDITY

Stomata serve to regulate the diffusion of water vapor out of a leaf and carbon dioxide into the leaf and thus play a primary role in controlling both photosynthesis and transpiration. It is now well known for a large number of species that the stomata of leaves are sensitive to changes in the leaf to air water vapor gradient (Δw), independent of changes in bulk leaf water status (Lange and others 1971; Schulze and Hall 1982). This response, often referred to as the stomatal sensitivity to humidity, is usually measured as the decrease in the leaf conductance to water vapor diffusion as the air becomes progressively drier. While numerous studies have documented differences in the stomatal sensitivity to humidity among species, few have attempted to correlate this parameter with plant performance or with plant distribution.

In their review, Schulze and Hall (1982) suggested that there was no systematic trend in stomatal sensitivity to Δw other than that those species which had the highest leaf conductances seemed to show the greatest absolute decrease in leaf conductance with increasing Δw . On the other hand, Losch (1979) and Losch and Tenhunen (1981) suggested in their reviews that although complete data sets were lacking there appeared to be a greater stomatal sensitivity to humidity in plants adapted to dry sites than in plants adapted to wetter sites. Furthermore, they

suggested that these differential sensitivities resulted in different rates of carbon gain in respective habitats and ultimately affected plant distributions. As evidence of this, Johnson and Caldwell (1976) compared stomatal sensitivity to increased Δw in four alpine tundra species, two adapted (=restricted?) to wet, moist sites and two adapted to drier, drained slopes. The stomates of the species adapted to wet sites were only slightly sensitive to decreased humidity, whereas leaf conductances of species from dry habitats decreased quickly in response to an increase in Δw . Supporting evidence for this pattern can also be seen in the comparative study of two *Diplacus aurantiacus* populations from coastal and inland habitats by Mooney and Chu (1983). In that study, leaves of plants of the population from the drier locations again had stomata that were more sensitive to changes in humidity than leaves of plants from the wetter habitat population.

GAS EXCHANGE AND WATER-USE EFFICIENCY

Since limited water availability is of major concern for the cultivation of crop plants and as well appears to limit the productivity of most if not all native plants, it is not too surprising that for many years there has been an intense interest in trying to understand how leaves simultaneously regulate carbon dioxide uptake and transpirational water loss (Tanner and Sinclair 1983; Sinclair and others 1984). Photosynthetic rates (A) tend to decline in response to a decreased leaf conductance (g), because carbon dioxide diffusion rates into the leaf and hence intercellular carbon dioxide concentrations (c_i) are progressively reduced with a reduction in leaf conductance. However, if leaf temperatures do not change substantially as the stomata close, there may be an increase in the water-use efficiency (molar ratio of photosynthesis to transpiration).

The rate of net photosynthesis as influenced by stomatal activity can be described as:

$$A = (c_a - c_i) g / 1.6 \quad (1)$$

and the transpiration rate (E) as

$$E = \Delta w g \quad (2)$$

where c_a is the atmospheric carbon dioxide concentration and 1.6 is the ratio of the diffusivities of water to carbon dioxide in air and is used to convert the conductance to water vapor through the stomata to the conductance to carbon dioxide through the stomata.

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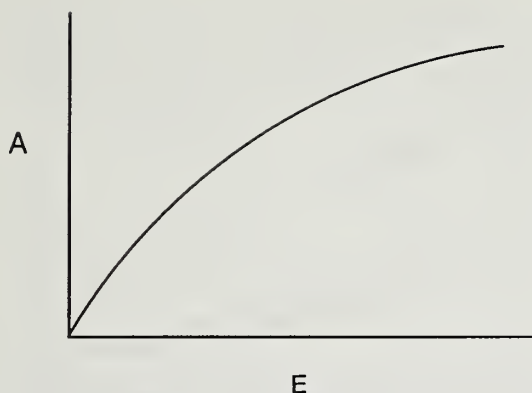


Figure 1--The relationship between net photosynthesis (A) and transpiration (E).

Combining these two equations we see that the water-use efficiency (A/E) becomes

$$A/E = (c_a - c_i)/(1.6 \Delta w) \quad (3)$$

Thus, under natural field conditions the leaf water-use efficiency depends on both the intercellular carbon dioxide concentration and the leaf to air water vapor gradient.

For a given decrease in stomatal or leaf conductance, the water-use efficiency of a leaf is typically increased (assuming leaf temperature remains constant). This is because a unit decrease in leaf conductance has a smaller impact on photosynthetic rate than it does on transpiration rate. In Figure 1, the relationship between A and E is plotted. Note that the relationship is curvilinear and that the slope of this relationship, which is water-use efficiency, decreases as the flux rates increase. The decrease in photosynthesis with decreased leaf conductance is best visualized by examining the dependence of net photosynthesis on intercellular CO_2 and the role that leaf conductance plays in regulating c_i values (Figure 2). While a unit decrease in leaf conductance results in a unit decrease in transpiration rate, its impact is smaller on photosynthesis because the A vs. c_i response curve is usually nonlinear and has a nonzero intercept on the x-axis (that is C_3 plants have a positive compensation point). In our analyses, we have assumed that the A vs c_i response curves were similar among the different oak species; preliminary data on leaf amino nitrogen contents of these species are supportive of this assumption (Ehleringer, Hogle and Blackmore, unpublished observations).

CARBON ISOTOPE RATIO

Measuring leaf water-use efficiency over long time periods has been difficult because of the necessity to simultaneously measure biomass production and water consumption in a nondestructive manner. However, Farquhar, O'Leary and Berry (1982b) first proposed an alternative means of estimating leaf water-use

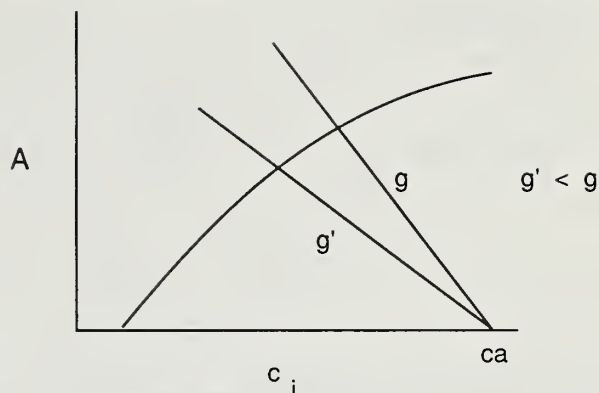


Figure 2--The dependence of net photosynthesis (A) on intercellular CO_2 concentration (c_i), often referred to as the "demand function" for photosynthesis. The linear lines represent the leaf conductance to CO_2 diffusion through the stomata, often referred to as the "supply function". The intersection of the demand and supply functions is the operational point, given those leaf characteristics. In this figure $g > g'$, so that the reduced leaf conductance of g' results in a lower intercellular CO_2 concentration and thus also a lower photosynthetic rate.

efficiencies using carbon isotope ratios at natural abundance levels.

The carbon isotope ratio ($\delta^{13}C$) is the ratio of the $^{13}C/^{12}C$ composition of a sample (R_{sample}) relative to the $^{13}C/^{12}C$ composition of a standard (R_{std}),

$$\delta^{13}C = (R_{sample}/R_{std} - 1) 1000 \quad (4)$$

where $\delta^{13}C$ has units of parts per mil (o/oo) and represents the deviation in composition of the sample from the standard, a fossil belemnite from the Pee Dee Formation (PDB).

Farquhar and others (1982b) proposed that there should be a relationship between the average c_i during the photosynthetically active period and $\delta^{13}C$. Their idea is based upon two observations: first $^{13}CO_2$ in air diffuses more slowly than $^{12}CO_2$, and second, that RuBP carboxylase, the initial carboxylating enzymatic reaction of photosynthesis in C_3 plants will discriminate against $^{13}CO_2$. While RuBP carboxylase can discriminate against $^{13}CO_2$, it does so only as a function of CO_2 levels actually at the sites where carboxylation is occurring (i.e., c_i level). Thus, it is predicted that

$$\delta^{13}C_{leaf} = \delta^{13}C_{air} - a - (b-a) c_i/c_a \quad (5)$$

where a is the discrimination due to diffusion differences (4.4 o/oo) and b is the discrimination due to RuBP carboxylase (27 o/oo). A number of data sets exist which verify the expected relationships between $\delta^{13}C$ and intercellular CO_2 (Farquhar and others 1982a; Bradford and others 1983; Ehleringer and others 1985).

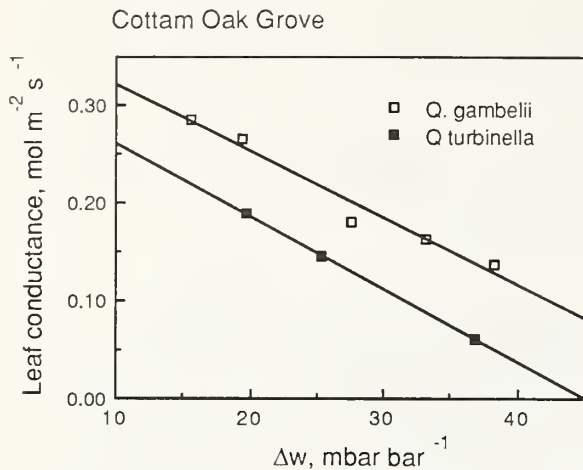


Figure 3--The dependence of leaf conductance to water vapor on the leaf to air water vapor gradient (Δw) for leaves of *Quercus gambelii* and *Quercus turbinella* under common field conditions in the Cottam Oak Hybrid Grove at the University of Utah.

The advantage of using stable isotopes is that since carbon is continually being fixed by a leaf, measuring the carbon isotope ratio of a leaf provides a long-term indication of c_i . Therefore, carbon isotope ratio is useful as a long-term indicator of leaf-water use efficiency (assuming leaf temperatures are held constant). Since various environmental factors (such as drought, temperature, salinity) influence gas exchange and thus c_i , carbon isotope ratios can be used to estimate how water-use efficiency changes in response to a diversity of environmental conditions.

OAKS IN THE COTTAM OAK HYBRID GROVE

In the 1960's Dr. Walter Cottam of the University of Utah began assembling a diversity of oak species from North America, Europe and Asia for experimental studies (Cottam, Tucker and Santamour 1982). His interest was in producing and examining various hybrid combinations, some of which might naturally arise in zones where the species naturally overlapped in distribution. Parents and hybrids from his studies have now been established for many years at an experimental garden (Cottam Oak Hybrid Grove) adjacent to the University of Utah campus.

In this paper, we examine the stomatal characteristics and carbon isotope ratios of three of the oaks, *Quercus gambelii*, *Q. macrocarpa*, and *Q. turbinella* and their hybrids. We have chosen these species as they represent the three most important oak species in the intermountain west, they occur in habitats of contrasting aridity and water availability, and in areas of overlap do indeed form hybrid zones.

The three oak species occur in contrasting ecological zones. *Q. gambelii* has deciduous leaves and occurs in relatively mesic zones

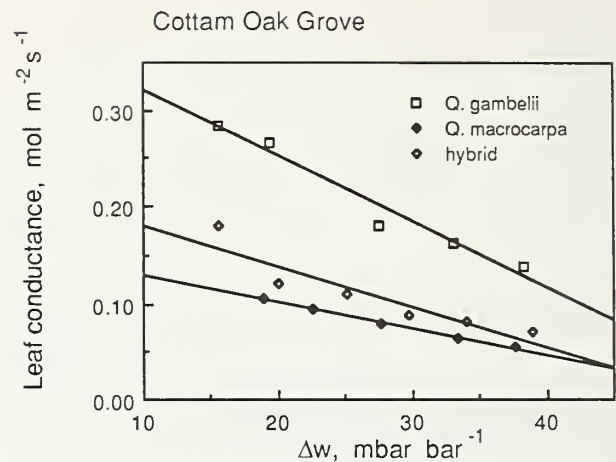


Figure 4--The dependence of leaf conductance to water vapor on the leaf to air water vapor gradient (Δw) for leaves of *Quercus gambelii*, *Quercus macrocarpa* and hybrids under common field conditions in the Cottam Oak Hybrid Grove at the University of Utah.

between grassland and coniferous forests, primarily in northern Arizona, Colorado and Utah. In the drier, more southern portions of Arizona, California, New Mexico and Utah, *Q. gambelii* is replaced by the evergreen-leaved species *Q. turbinella*. *Q. macrocarpa* occurs on the eastern margins of the intermountain west and its distribution extends across much of the Great Plains region. It is a deciduous-leaved species, effectively restricted to riparian habitats.

STOMATAL SENSITIVITY TO HUMIDITY IN OAKS

Stomatal responses to changes in humidity between a Δw of 20 and 40 mbar bar⁻¹ were essentially linear in all oak species examined. The major differences between species were due to changes in the slopes and intercepts of these relationships. The stomata of *Q. turbinella* were more sensitive to changes in Δw than were the stomata of either *Q. gambelii* or *Q. macrocarpa* (Figures 3-4). On average the change in leaf conductance per unit change in Δw ($\delta g / \delta \Delta w$) was -0.077, -0.066, and -0.024 for the three species respectively (Tables 1-2).

In the crosses between *Q. gambelii* and *Q. turbinella*, the performance of the hybrids was reduced below that of either parent (Table 1). Both the slope and intercept of the leaf conductance versus Δw response curve were very much lower in magnitude.

For the crosses between *Q. gambelii* and *Q. macrocarpa*, the stomatal behavior of the hybrids was intermediate between that of the parents (Table 2). Both the slope and the intercept of the leaf conductance versus Δw response curve were intermediate between the two parents.

There was no significant correlation among species and hybrids between the slope and

Table 1--Mean slope ($\text{mol bar mbar}^{-1} \text{ m}^{-2} \text{ s}^{-1}$) and intercept ($\text{mol m}^{-2} \text{ s}^{-1}$) values for the dependence of leaf conductance to water vapor on the leaf to air water vapor gradient (Δw) for Q. gambelii, Q. turbinella and hybrids between them growing in the Cottam Oak Hybrid Grove at the University of Utah

	<u>Q. gambelii</u>	<u>Q. gambelii x turbinella</u>	<u>Q. turbinella</u>
slope	-0.066	-0.0030	-0.077
intercept	0.380	0.275	0.350

Table 2--Mean slope ($\text{mol bar mbar}^{-1} \text{ m}^{-2} \text{ s}^{-1}$) and intercept ($\text{mol m}^{-2} \text{ s}^{-1}$) values for the dependence of leaf conductance to water vapor on the leaf to air water vapor gradient (Δw) for Q. gambelii, Q. macrocarpa and hybrids between them growing in the Cottam Oak Hybrid Grove at the University of Utah

	<u>Q. gambelii</u>	<u>Q. gambelii x macrocarpa</u>	<u>Q. macrocarpa</u>
slope	-0.066	-0.0042	-0.024
intercept	0.380	0.224	0.157

intercept of the leaf conductance versus Δw response curve. The independence of these two characters suggests that leaves of species with intrinsically higher gas exchange rates are not necessarily more sensitive to changes in Δw than leaves of species with lower gas exchange rates.

WATER-USE EFFICIENCY IN OAKS

There was a large intraspecific variation in long-term water-use efficiencies as indicated by leaf carbon isotope ratios for both Q. gambelii and Q. turbinella (Figure 5). For both species, there was slightly more than a 2 o/oo range in carbon isotope ratios values. This suggests that mean $\delta^{13}\text{C}$ values among genotypes of each species differed by more than 30 $\mu\text{l l}^{-1}$. Unfortunately as there was only a single Q. macrocarpa tree within the experimental garden, it is not possible to say much about the variation within this species.

The impact of the changes in $\delta^{13}\text{C}$ on actual water-use efficiency will depend on the atmospheric humidity conditions. If we assume typical daytime summer values for Salt Lake City of 32 C for both air and leaf temperatures and a 20% relative humidity, then the calculated change in water-use efficiency in going from a carbon isotope ratio of -27 o/oo to -25 o/oo is an increase of 25%, increasing from an absolute value of 1.47 to 1.84. Thus, there would appear to be substantial genetic variation in water-use efficiency within oak genotypes. The implications of these differences in water-use efficiency to long-term plant performance are not understood at this time.

The hybrids growing in the Cottam Oak Grove also exhibited a wide variation in leaf carbon isotope ratios (Figures 5-6). For the crosses between Q. gambelii and Q. turbinella, there was as much isotopic variation as in each of the parents and the values overlapped completely with the range of Q. turbinella. However, for the Q. gambelii and Q. macrocarpa crosses, even though the range of leaf isotope ratios of the hybrids was similar to the parents (at least of the Q. gambelii parent), the mean isotope ratios were intermediate between those of the two parents (given the limited data available for Q. macrocarpa).

CORRELATIONS BETWEEN WATER RELATIONS AND OAK DISTRIBUTION

In the intermountain west, Q. gambelii occupies wetter, higher elevation sites than does Q. turbinella. It is then not too surprising to note that leaf carbon isotope ratio data suggest that water-use efficiency is higher in Q. turbinella than in Q. gambelii. What is perhaps surprising is the observation that water-use efficiency in Q. macrocarpa, a species which occupies riparian habitats is so much higher than that of Q. gambelii. Whether these differences are due to water conditions in the experimental garden or whether Q. macrocarpa has an intrinsically higher water-use efficiency is unclear at this time. The leaf carbon isotope ratio data for the Q. gambelii x macrocarpa and Q. macrocarpa x gambelii hybrids do suggest that Q. macrocarpa may indeed have a higher water-use efficiency under natural field conditions.

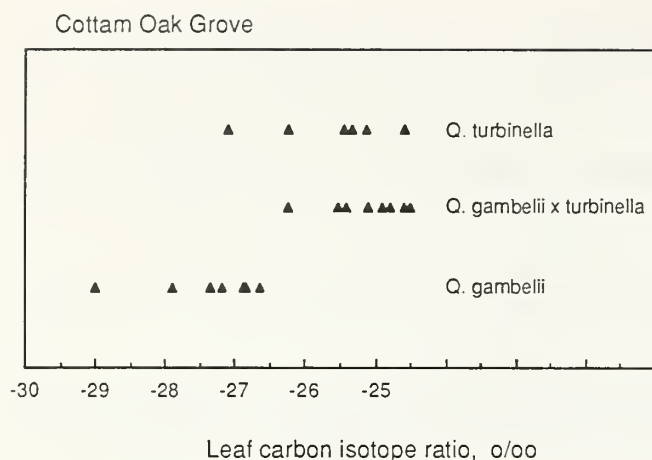


Figure 5--Leaf carbon isotope ratios for leaves of different individual trees of *Quercus gambelii*, *Quercus turbinella*, and hybrids between them at the Cottam Oak Hybrid Grove.

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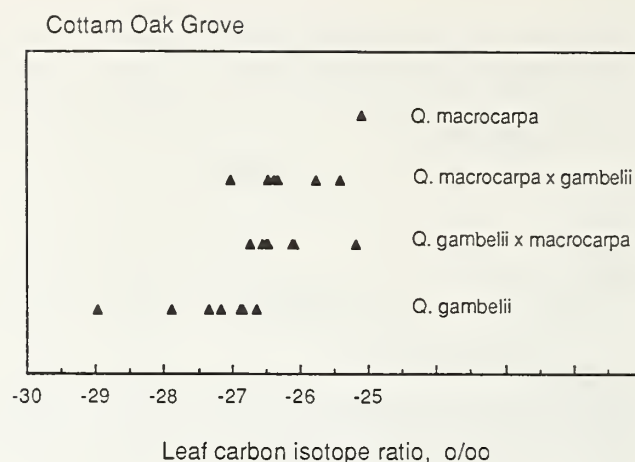


Figure 6--Leaf carbon isotope ratios for leaves of different individual trees of *Quercus gambelii*, *Quercus macrocarpa*, and hybrids between them at the Cottam Oak Hybrid Grove.

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PLANT ECOPHYSIOLOGY: A CASE STUDY OF HONEY MESQUITE //

R. E. Sosebee and C. Wan

ABSTRACT: Plant ecophysiology is often used interchangeably with "environmental physiology" and "physiological ecology". Ecophysiology is primarily concerned with "the physiology of plants as it is modified by fluctuating external influences". Species and ecotypes within species have their ranges of ecological adaptation based upon the physiological constitution of the plants. Xerophytes respond to the environmental conditions of their natural habitat similarly to mesophytes in their habitat.

Honey mesquite is a facultative phreatophyte. Its consumptive water use is very opportunistic. Transpiration rates and duration of transpiration are greater on wet sites than on dry sites. Predawn leaf water potentials are substantially higher in trees growing on wet sites (-12 bars) than in those on dry sites (-24 bars) during the summer drought. Photosynthetic rates are also higher in trees growing on wetter sites. Soil temperature influences growth and development of mesquite. Optimum temperature for root growth appears to be about 27°C. At sub-optimum temperatures (21°C) niacin appears to be limiting root growth and at supra-optimum temperatures (32°C) thiamine appears to be limiting. Mesquite anatomy responds to environmental changes. As the growing season progresses and the environment becomes hotter and drier, the leaves develop a thickened epidermal cell wall that reduces evapotranspirational water loss.

Native plants are well adapted to the environment in which they have evolved. Their physiological mechanisms allow them to take advantage of the existing conditions. All species (and all ecotypes or populations within a species) do not respond to the same environment in the same manner. The physiological response of each species and ecotype should be evaluated for each environment in which the plant grows to fully understand its ecophysiology.

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INTRODUCTION

Plant "ecophysiology" is often used interchangeably with "environmental physiology" and "physiological ecology" depending upon one's background (Tracy and Turner 1982). Plant ecophysiology is primarily concerned with "the physiology of plants as it is modified by fluctuating external influences" (Larcher 1980). Emphasis of physiological relationships in plant ecology is not new. Schimper (1898) was one of the first to suggest that ecological relationships be approached from a physiological viewpoint. Tansley (1914) suggested that the most fundamental problems of plant ecology were physiological and called for the formation of a School of Physiological Ecology to address the basic issues of ecology.

The physiological approach to ecological problems seems to have been largely abandoned until the 1960's. In 1962 an international symposium was held in Montpellier, France to address ecophysiological problems of arid zone research (Eckardt 1965). This symposium served as the springboard for renewed interest in plant ecophysiology or physiological ecology. Since the mid 1960's, there has been a major emphasis on plant ecophysiology.

"Normal" and "extreme" ranges of environmental factors vary in time and space. The diversity of species exploiting any particular environment reflects specific adaptations of the species. The nature of these adaptations must be examined in view of the plant's physiological ability to respond to the environment (Fitter and Hay 1981). Favorable environmental conditions are not necessarily determined by regional climates or even microclimates. Adaptability is determined by the environment in which the vital processes take place within the protoplasm (Walter 1973). Largely, a plant's adaptability to specific environments depends upon its enzyme and membrane responses to the internal conditions created by the external environment.

This presentation is intended as an overview of plant ecophysiology. Time and space do not permit a thorough treatise on plant ecophysiology. Everyone has a basic understanding of plant ecological and physiological processes; therefore, specific examples will be drawn from honey mesquite (*Prosopis glandulosa*) on how a plant responds physiologically to its environment.

One of the common mistakes made by plant physiologists and plant ecologists is assuming that all populations within a species respond similarly to all environments within the species'

range. Turresson (1922a, 1922b) demonstrated differences among populations within a species according to habitat differences which he called ecotypes. Classical ecotypic differentiation within *Achillia* and *Potentilla* has been shown by Clausen and others (1940). Since the early 1940's others have shown ecotypic differentiation within a number of species (McNaughton 1966, McNaughton 1967, McNaughton 1972, Davies and Snaydon 1973a, Davies and Snaydon 1973b, Davies and Snaydon 1974, Goodman and Caldwell 1971, Musselman and others 1975, Vickery 1950, Wilkinson 1980, Whalley and Burfitt 1972, Wooten 1973, and Workman and West 1969). Ecotypes may or may not be morphologically distinct, but they are genetically different. They respond differently to similar environmental regimes according to their physiological capabilities.

Ecotypic variation in mesquite has only briefly been addressed. *Prosopis* has a wide distribution ranging from much of North and South America, to North Africa and the Middle East (Simpson and Solbrig 1977). Ecotypic variation was demonstrated among North American species by Peacock and McMillan (1965). They showed that populations of *P. glandulosa* responded to photoperiod, thermoperiod, and length of growing season according to the latitude from which they were collected. McLendon (1979) further showed that edaphic ecotypes exist within *Prosopis glandulosa*. It is important for scientists to realize that plants within a species will have different physiological responses to an environment depending upon their evolutionary history. If one chooses to undertake an ecophysiological study of a species, he must first identify the environment which that species inhabits.

SEEDS AND SEEDLINGS

Physiological response to any environment varies seasonally, annually, and throughout the life cycle of the plant. Mature seeds are the most resistant organs to environmental change; however, maturation of fruits and seeds is quite vulnerable to environmental conditions.

Germination of seeds and establishment of seedlings depends upon several factors. Harper and others (1961) have referred to the summation of these factors as "safe sites". Safe sites imply adequate water, appropriate temperatures and light, and sufficient space are available for germination to occur and seedlings to be established.

Soil temperature and water potentials are critical to the germination process. Water is essential to initiate germination. Seeds of native, wildland plants have a very low water content (<15%) and will remain dormant until the environment receives adequate water to assure the germination process (McDonough 1977). When sufficient water is received, as perceived by the seed resulting from scarification, leaching inhibitors, etc., imbibition will occur releasing gibberellic acid from the aleurone layer in the seedcoat initiating the biochemical reactions of the germinating process.

Amount of water required for germination varies among species depending upon their adaptations. However, there is a minimum threshold in water content that must be surpassed before germination will begin. After germination is initiated, a minimum amount of water must be maintained in the environment to insure completion of the germination process and establishment of the seedlings. Several scientists (Wester and others 1986, Frasier and others 1985) have illustrated the importance of continuous soil moisture in establishment of kleingrass (*Panicum coloratum*), weeping lovegrass (*Eragrostis curvula*), Lehmann lovegrass (*E. lehmanniana*) and "Cochise" lovegrass (*E. lehmanniana* ssp. *E. trichophora*). Their research pointed out that the amount of soil water is not as important to germination and establishment as the constancy of the supply. Much research in Colorado (Hyder and others 1971, Wilson 1971, Hyder and others 1976, Wilson and others 1976, Briske and Wilson 1977, Briske and Wilson 1978, Wilson and Sailes 1978, Wilson and Briske 1979, Briske and Wilson 1980, and Fulbright and others 1985), illustrates the importance of soil water in establishment of blue grama (*Bouteloua gracilis*), crested wheatgrass (*Agropyron cristatum*) and green needlegrass (*Stipa viridula*).

Usually, plants adapted to drier climates develop an extensive root system before shoot growth begins. A sand shinnery oak radicle will easily be two-feet long before the cotyledons emerge from the seed (R. D. Pettit, personal communication). Mesquite undergoes similar development phases in the germination process (Mooney and others 1977). Root development in both *P. velutina* and *P. glandulosa* greatly exceeds shoot development.

Soil temperature is also very important in germination and seedling establishment of mesquite. High soil temperatures hinder seedling establishment as well as low temperatures. Grass and shrub seeds have very low germination and establishment rates under high temperature regimes such as those found in the desert southwest. Reduction of soil temperature from an average of 40°C, or higher, to 26°C increased establishment of fourwing saltbush (*Atriplex canescens*), sacaton (*Sporobolus wrightii*), vine mesquite (*Panicum obtusum*), and bush muhly (*Muhlenbergia porteri*) (Sosebee and Herbel 1967).

Optimum temperature for germination of mesquite seeds is 85°F and the minimum threshold is 77°F; germination was reduced at 100°F (Haas and others 1973). Amount of soil water required for germination varied according to the soil temperature; less water was required for germination at 85°F than at either 70° or 100°F (Haas and others 1973). Germination rates were not reduced by water potentials of 8 atm, as long as the temperature was 85°F. Water stress apparently occurred at 100°F, whereas, temperature adversely affected germination at 70°F.

Light is an important influence in seed germination. Early successional plants are often classified as r-selected species which refers to an intrinsic rate of natural increase; whereas, climax plants are classified as K-selected species (Barbour and others 1987). The r-selected plants

usually are adapted to high light regimes and require light for germination. Since K-selected species are climax species, they do not require light for germination; and, in fact, may be inhibited by sunlight during the germination process. Mesquite seedlings emerged and became established with 50% reduction in solar radiation, but survival was significantly reduced when radiant energy was reduced 75% or more (Scifres and others 1973). Fisher and others (1959) found that if grass cover is severely disturbed, chance of mesquite seedling establishment is substantially increased.

Germination of mesquite seeds under rangeland conditions varies from laboratory tests. Mesquite seeds are encased within very fibrous pods and are characterized by extremely hard seed coats. Mesquite seed germination is significantly enhanced after it passes through the digestive tract of an animal or is scarified by some other means. Ueckert and others (1979) found quite high emergence rates (17.4 - 47.0%) under field conditions, but survival rates were usually low (Ueckert and others 1979, Meyer and Bovey 1982). Most native plants have similar protective mechanisms that ensure survival of the population under unusual or adverse climatic conditions. Any population risks demise if all seeds germinate at the same time under similar environmental conditions. Seed polymorphism is important to the establishment and survival of seedlings and persistence of the population (Palmlblad 1968a, 1968b, Harper and others 1970).

The seedling stage of all plants is the most vulnerable stage in the life cycle. Survival of seedlings depends upon the ability of the radicle to grow in wet soil which is very critical since the surface soil usually dries very rapidly. Seedlings are very susceptible to water stress because of the lack of development of anatomical and morphological features that conserve water.

It appears that seed germination and seedling emergence are among the most critical stages in plant succession. Seemingly, plant succession does not occur gradually along a gradient, especially in semiarid and arid climates, but rather, it occurs in spurts. Environmental conditions are not always conducive for seed germination and seedling establishment. Creosotebush (*Larrea tridentata*) that occupies much of the Southwest ranges and dominates many plant communities on the Jornada Experimental Range in southern New Mexico has not always enjoyed the geographic distribution that it now occupies. The first major influx of creosotebush into present day communities occurred in the early 1940's with above average rainfall (C. H. Herbel, personal communication). Several successive days of wet weather must accompany above average rainfall years for creosotebush to become established. Once it becomes established, however, few species can compete with it. Similar expansion of mesquite into communities that it now dominates has been observed following above average rainfall years in the 1960's.

PHENOLOGICAL DEVELOPMENT

Phenology (derived from Greek "phainein" which means "to show") is the study dealing with relations between climate and periodic biological phenomena. Phenological development is the progression of stages of growth during the annual cycle.

Plants spend the winter in some degree of resting. Much research has been devoted to resting phases of fruit trees and break of dormancy in the spring. Bud and tiller formation seem to occur during the spring and fall preceding the year in which they will be expressed. Environmental conditions during formation of buds and tillers directly affect biomass production the following year. Mesquite foliage is very dense in springs following a wet spring and fall the preceding year; whereas, less foliage is produced when the preceding spring and fall are dry. Budbreak in the spring is dependent on photo- and thermoperiods. Budbreak in indigenous plants and onset of dormancy are governed by their evolutionary history (Peacock and McMillan 1965). Goen and Dahl (1982) found that minimum air temperatures January through March and the number of days that the minimum fell below freezing dictated timing of budbreak of mesquite in west Texas. Regardless of temperatures, budbreak rarely occurs before the photoperiod exceeds 11.5 hours. Twig elongation in mesquite begins when the soil temperature reaches 65-70°F and continues for approximately 6 weeks (Haas and others 1973).

Apical dominance is an old concept regulating growth and development of all plants. Apical meristems are small, but they dictate the growth habit of all plants, both herbaceous and woody. Excellent reviews are provided by Romberger (1963) and Dahl and Hyder (1977). Theoretically, plants can live as long as the apical meristem is active. Once it is damaged or destroyed, the shoot dies. Many herbaceous and woody plants produce lateral buds that remain inactive until apical dominance is destroyed or they can produce adventitious buds.

Many of our difficult to control weedy perennials (herbaceous and woody plants) are sprouters; i.e., they sprout from lateral or adventitious buds following destruction of apical dominance. Silverleaf nightshade (*Solanum elaeagnifolium*) produces a massive root system which has given rise to debate whether most of the biomass is roots or rhizomes. Once a shoot is destroyed, new shoots can arise from any portion of the root segment that is in a favorable soil environment (Stubblefield 1986). Mesquite responds similarly to loss of apical dominance. Mesquite sprouts from basal buds that arise from the buried cotyledonary node (Fisher and others 1946, Morey and Dahl, 1975) and dormant bud traces immediately below the bark (Haas and others 1973).

Growth of mesquite resprouts depends largely upon the time when apical dominance is removed. Plants with shoots that are damaged or mechanically destroyed (chemically or mechanically) during dormancy, sprout the following spring with great vigor. Often these sprouts will develop rapidly

and flower the first growing season. If shoots are destroyed during the wet portion of the growing season when the root carbohydrate level is high, the plants will sprout rapidly, but usually the sprouts will not flower the same growing season. If, however, apical dominance is destroyed during a dry portion of the growing season or the root carbohydrate level is low, sprouting is suppressed for some time, perhaps as long as 3 to 5 years. Time of the year, phenological stage and environmental conditions at the time apical dominance is destroyed has more influence on sprouting and flowering of the resprouts than number of years post-destruction (Beck and others 1975). Flowering depends upon whether the sprouts produce long or short shoots (Dahl and Hyder 1977).

Native plants are uniquely adapted to their environment. Most produce more flowers than the plant can support if all matured into fruits and seeds. Annuals produce large numbers of seeds with tremendous variability. It has been suggested that one method of controlling annual plants is to mow them before seeds are produced. Species such as rescue grass (*Bromus unioloides*) and dandelions (*Taraxacum officinale*) will produce seeds at or below the surface of the soil. Many fruits are produced that abort before maturation (Stephenson 1981). Mesquite trees produce numerous flowers, but very few fruits per spike. Goen (1975) found that in the Rolling Plains of Texas some trees produced pods every year and some never produced pods. Production of pods varies from year to year. An old adage suggests that if mesquite trees produce many beans (pods), the year will be dry. Perhaps this is a survival mechanism for the population and there is some truth to the adage, although it is undocumented scientifically.

ROOTING HABITS

Most xerophytes and phreatophytes have the reputation of having deep taproots. However, it has been suggested that most of the xerophytes rely on a shallow lateral root system more than the deep taproot. Mesquite has a deep taproot 5 to 13 m (Fisher and others 1959) and even to depths of 58 m (Phillips 1963). It has an extensive lateral system with radii extending to 17 m (Fisher and others 1958, Cable 1977).

Recent evidence indicates that the most active laterals occur in the upper 75 cm of soil. Dahl and others (1971) and Dahl and Sosebee (unpublished data) have found that the most important environmental factor contributing to control of mesquite with foliar applied herbicide is soil temperature at depths between 30 and 60 cm. Transpiration was unaffected in trees with taproots severed at 75 cm if surface of the soil was wet, but it was significantly reduced when the upper 75 cm became dry (Thomas and Sosebee 1978). These results suggest that the deep taproot plays a significant role in water uptake only during extended droughts when surface moisture is lacking. Bedunah (1982) found annual forbs such as sunflower (*Helianthus annuus*), and Russian thistle (*Salsola kali*) growing in and around pits created by grubbing (and removing) mesquite. Where pits

were made by grubbing between the trees (with the trees left intact), no forbs grew, indicating competition from mesquite for soil water. Similar rooting behavior in mesquite has been observed by Jacoby and his coworkers (P. Jacoby, personal communication).

Although many plants have deep taproots and extensive lateral roots, they depend largely upon their shallow roots for most active absorption. In the dry southwestern and western parts of the U.S., dependence upon shallow roots is advantageous allowing plants to utilize the limited precipitation that infiltrates the soil. Reliance of xerophytes upon deep root systems is disadvantageous because of the depth to available water.

PHOTOSYNTHESIS AND TRANSPIRATION

Honey mesquite has high photosynthetic rates in semiarid and arid environments. Mooney and others (1977) found that at intercellular CO_2 concentration of $250 \mu\text{l l}^{-1}$, the measured photosynthetic rates for mesquite in the Sonora Desert were over $30 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. Daily maximum CO_2 exchange rate of $28.6 \text{ mg dm}^{-2} \text{ hr}^{-1}$ was reported by Dye and Hanson (1978) for semiarid Trans-Pecos Region of west Texas and CO_2 uptake rate of $32.9 \text{ mg dm}^{-2} \text{ hr}^{-1}$ was measured by Meyer and others (1982) for Bryan, Texas. At the Texas Tech campus, Lubbock, Texas, with a ambient CO_2 concentration of a $350 \mu\text{l l}^{-1}$, we measured a daily maximum photosynthetic rate of $33.54 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ in June. Following heavy precipitation the CO_2 exchange rate was even higher ($41.2 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$).

According to Larcher (1980), photosynthetic capacity ranged from 6 to $20 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ for desert shrubs and from 15 to $25 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ for sun leaves of winter deciduous trees. Therefore, photosynthetic capacity of mesquite exceeds the value for either the desert shrubs or the winter deciduous trees. It is similar to those of most C_3 crop plant species ($20\text{--}45 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$).

High photosynthesis of mesquite is probably related to its high leaf nitrogen content. In June, leaf Kjeldahl nitrogen contents can reach as high as 27 mg/g of the dry weight, which is equivalent to over 16% crude protein content. This value is close to the leaf nitrogen content of many desert winter annuals which are characterized by very high photosynthetic capacity (ranges from 28.15 to $103 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$) (Werk and others 1983). The high leaf nitrogen content is associated with nitrogen fixation capability of honey mesquite. Several fold increase in soil nitrogen and organic matter content under mesquite canopy has been found by many people (Arthur and others 1972, Rundel and others 1982, Virginia and Jarrell 1982, Shearer

and others 1983). The nodules were observed after a rain or in the soil layer where adequate soil moisture exists. This may partially explain the very high photosynthetic capacity of mesquite after the spring rainfall events.

Under favorable conditions, mesquite trees are not photosynthetically light saturated until a high irradiance level is reached. Hanson (1982) reported that light saturation point for mesquite was $1.78 \text{ mmol m}^{-2} \text{ s}^{-1}$ (400-700 nm radiation). In west Texas, this irradiance level is usually reached by 11:00 A.M. in June. In our field experiments, peak photosynthesis appeared between 11:00 A.M. - 2:00 P.M. after a heavy spring precipitation; and during this period, the quantum flux density was usually close to full

sunlight ($1.8\text{-}2.2 \text{ mmol m}^{-2} \text{ s}^{-1}$). It is clear that honey mesquite requires high light intensity to achieve maximum photosynthetic rates. This is in contrast with many other C_3 plant species

which are usually light saturated at 1/3 to 1/2 of full sunlight. The high light saturation requirement of honey mesquite resembles most C_4

plants and many desert species including ephemerals which have extremely high photosynthetic capacities. High light saturation point, high leaf nitrogen content and extensive rooting habit enable honey mesquite to successfully compete against many native species including some C_4 grass species such as bluegrama

and buffalograss (*Buchloe dactyloids*). In hot and arid environments, photosynthetic rates of C_4 plants are generally greater than those of C_3

plants. However, this may not necessarily be correct in all situations. Although honey mesquite is a C_3 plant, its photosynthetic capacity is within the range of C_4 plants ($30\text{-}80 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, Larcher 1980).

When soil water is not limited and relative humidity is high, photosynthesis of honey mesquite is mostly dependent upon light intensity. Daily maximum photosynthesis usually occurs at irradiance close to full sunlight. So does stomatal conductance. Photosynthesis and stomatal conductance increase almost linearly in the morning hours as irradiance increases. Then a depression occurs in the afternoon (fig. 1).

The diurnal curve exhibits a close coupling between photosynthesis and leaf conductance. This means that any increase in leaf conductance is associated with an increase in CO_2 uptake in the morning hours and suggests that the plant is photosynthesizing at least expense of transpirational water loss. In the meantime, the plant is able to maintain a relatively constant intercellular CO_2 concentration at about $250\text{-}270 \text{ } \mu\text{l l}^{-1}$.

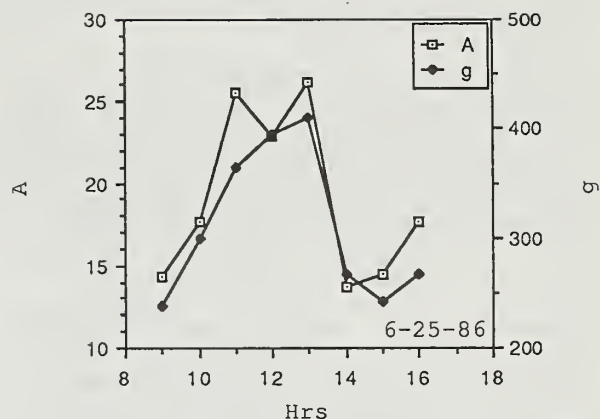


Figure 1--Diurnal photosynthesis (A , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and conductance (g , $\text{mmol m}^{-2} \text{ s}^{-1}$) pattern during a wet period. Note the depression in A at 2:00 p.m. is accompanied by the decrease in g .

In a drought period, the morning photosynthesis of honey mesquite is not only dependent upon the irradiance levels, but also restricted by edaphic and atmospheric drought. Peak photosynthesis occurs several hours earlier than in the wet period. The magnitude of peak photosynthetic rates is also substantially reduced, and usually declines by half with a moderate soil water deficit and by 3-fold with a severe water stress. During wet periods, photosynthesis and leaf conductance are very responsive to irradiance levels; however, they become less responsive to irradiance in the drought period because water stress plays a major role in limiting CO_2

fixation. In drought periods, photosynthesis and leaf conductance of mesquite are influenced, to a large extent, by vapor pressure deficit (VPD) and soil water deficit. The stomata start to close at VPD exceeding about 30 mbars.

Depression in photosynthesis of mesquite under water stress conditions has been attributed mainly to stomatal closure (Dye and Hanson 1978, Hanson 1982), which was thought a result of decreased plant water potentials. In our experiments, it appeared that major limitation on photosynthesis of mesquite was not attributed to stomatal closure. In drought periods, stomatal conductance was much reduced, which caused the intercellular CO_2

concentration to become much lower than that in the wet period (average around $150\text{-}180 \text{ } \mu\text{l l}^{-1}$). However, with a similar internal CO_2 concentration, the trees growing on more mesic clay loam sites had photosynthetic rates 2-fold higher than the trees growing on xeric sandy loam sites. The midday depression in photosynthesis usually was not associated with lower internal CO_2 concentration, it was often higher instead. This indicates that under water stress conditions, the ability of mesophyll cells to fix CO_2 is reduced, which causes the internal CO_2 concentration to increase. Thus, instead of stomatal closure causing reduced photosynthesis, stomata of mesquite seem to

respond to reduced photosynthesis and increased internal CO_2 concentration.

Our data further indicate that neither photosynthesis nor stomatal conductance is highly associated with xylem water potentials. In wet periods, the plants photosynthesized at high rates with stomata widely open, yet the xylem water potential was low. Likewise, during drought conditions, photosynthesis declined to a low level. So did stomatal conductance; but xylem water potential increased. There is nothing unique about xylem water potential regarding photosynthetic rate. Our data show that mesquite trees can maintain a positive carbon balance at xylem water potential of -40 bars, but sometimes net photosynthesis dropped to zero at xylem water potential of -34 bars. In midsummer, mesquite growing on the more mesic sites achieved greater photosynthetic rates than the trees on the xeric sites; but, we found no difference in xylem water potential between the two sites. Lack of correlation between photosynthesis and xylem water potential suggests that xylem water potential may be of minor importance in affecting photosynthesis of mesquite.

Seasonal change in photosynthetic capacity of mesquite is tightly correlated with soil water availability. For two consecutive years, we found a significant linear relationship ($r=0.89$; $p=0.001$) between daily maximum photosynthesis and soil water content at the 30 to 60 cm depth on a fine sandy loam (fig. 2).

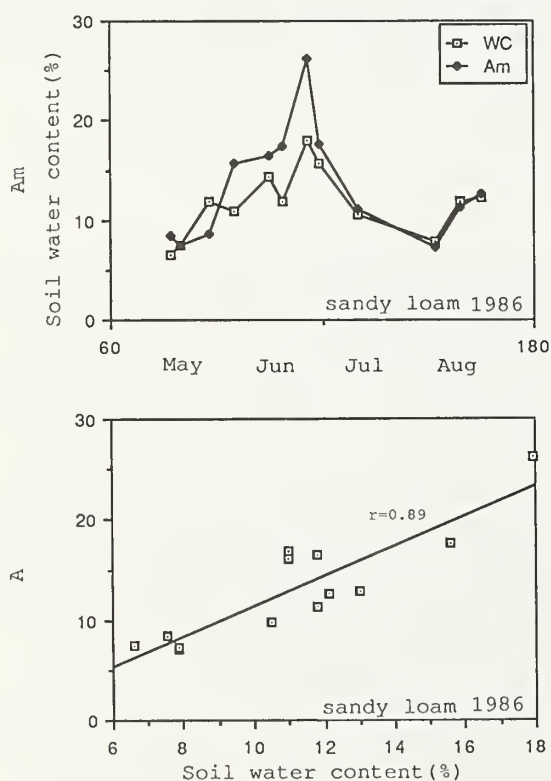


Figure 2--Upper: Seasonal change of daily maximum photosynthesis (A_m , $\mu\text{mol m}^{-2} \text{s}^{-1}$) as affected by soil water content (w/w). Lower: Relationship between A_m and soil water content. $P=0.001$.

The average photosynthetic rates were also related to soil moisture levels. This provided evidence that the major site for the plant to "sense" water stress is the root system, as recently suggested by Turner (1986).

Although honey mesquite is considered a phreatophyte, its photosynthetic capacity is susceptible to soil water availability. This further confirms that honey mesquite in west Texas is not a true phreatophyte, but a facultative phreatophyte (Thomas and Sosebee 1978). It primarily depends on moisture held in the upper soil horizon for its physiological requirement. Whereas, the taproot is not functional until water in the surface soil is depleted.

Wendt and others (1967) found that transpiration and growth of mesquite seedlings in a greenhouse were affected by soil temperature. Our field data suggest that photosynthesis of honey mesquite is also influenced by soil temperature when soil moisture is not limiting. On a clay loam site near a playa where seasonal changes in soil moisture were minimal, photosynthetic capacity of mesquite during the spring rainy season mainly responded to soil temperature regime and soil aerobic conditions. The greatest photosynthetic rates occurred when the soil temperature at 45 cm was relatively high ($23\text{--}24^\circ\text{C}$) and soil moisture content was about 70-80% of field capacity. However, when soil was saturated after a heavy rainfall and soil temperatures dropped to 21°C , photosynthesis declined. This response of photosynthesis to soil temperature was observed for 2 years. Low soil temperature and anaerobic conditions apparently colimit photosynthesis. Whether the effect is direct or indirect needs further investigation.

The temperature optima for photosynthesis of mesquite ranges from 27°C to 31°C , which fall in the upper range of optimum temperature for C_3 plants ($20\text{--}30^\circ\text{C}$). Similar data were presented by Dye and Hanson (1978), Hanson (1982), and Meyer and others (1982). This temperature optima for photosynthesis is very similar to the optimum soil temperature (29°C) for root function. However, there is a seasonal shift in optimum temperature for honey mesquite. In late October and early November, the daily peak photosynthesis occurred at air temperatures from 14 to 18°C . When quantum flux density approached $1.2 \text{ mmol m}^{-2} \text{s}^{-1}$ and air temperature further increased to over 20°C , photosynthesis declined. Available soil water content was not limited in this period. This change in temperature optima may reflect temperature acclimation of mesquite when the plant is subjected to a low temperature environment.

The ability to acclimate to a low temperature environment has ecological significance. It can extend the growing season for honey mesquite and enhance its competence. Most C_4 plants cannot tolerate low temperatures and are not active photosynthetically when the temperature drops to about 10°C . In contrast, honey mesquite can achieve peak photosynthesis at 14°C after occurrence of the first frost. In west Texas, most C_4

species start growth a month later than mesquite and stop photosynthesizing much earlier than mesquite. This makes the growing season for mesquite much longer than its C_4 counterparts and enables the plant to more efficiently use available resources.

Honey mesquite is also capable of acclimating to high temperature regimes. Thermal stability of the plant increases as the season progresses. On hot afternoons, zero CO_2 exchange is observed in the native habitat because of inhibition caused by high leaf temperatures and water stress. Ability of the plants to deal with high temperature stress is associated with the length of time the tree is exposed to a high temperature environment. In mid June, zero net photosynthesis occurred at a leaf temperature of $37^\circ C$ in the light green leaf stage while positive CO_2 exchange rate was obtained at $39^\circ C$ in the dark green leaves. In late July, the plants maintained a positive net assimilation rate at a leaf temperature of $42.5^\circ C$.

A linear relationship between photosynthesis and leaf conductance existed in mesquite trees ($P = 0.001$, $r = 0.7$ to 0.84 , $n = 130$) across different environmental conditions (fig. 3).

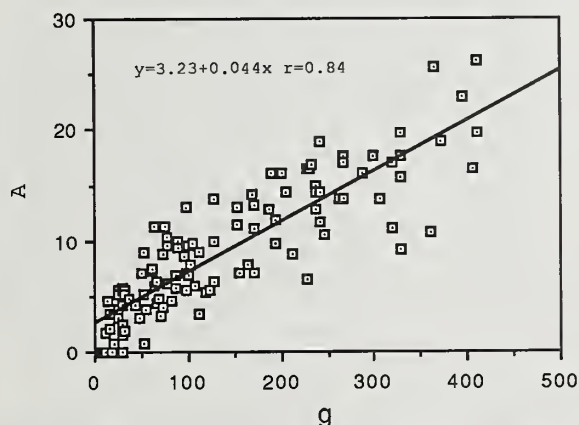


Figure 3--Relationship between photosynthesis (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and leaf conductance (g , $\text{mmol m}^{-2} \text{s}^{-1}$) in honey mesquite in Lubbock, Texas ($n=130$, $P=0.0001$).

This relation has revealed that the plant can achieve maximum water use efficiency (WUE) in its native habitat. Mesquite is not wasteful in terms of water cost per unit carbon gained. Even when soil water is most available, the plant does not use water extravagantly as many have thought. In wet periods, honey mesquite can have a water use efficiency of $9.7 \text{ mg } CO_2 / \text{g } H_2O$, which is similar to that of some C_4 plants (Caldwell and others 1978). This high WUE is attributed to high photosynthetic rates when soil water is adequate. High WUE is also due to stomatal regulation on transpirational water loss. When the environment favors plant growth as in June, stomata are open and transpirational water loss is high, but the plants fix as much CO_2 as possible. When the high

VPD promotes transpiration, as in July, photosynthesis is inhibited. As a consequence, stomata are closed, so extra water loss can be prevented. Therefore, seasonal WUE of honey mesquite tends to approach maximum. Diurnal WUE remains relatively constant. This kind of stomatal behavior is optimal in a semiarid environment; it allows the plant to better adapt to the water limited habitat. It provides another explanation for the expansion of honey mesquite into the semiarid Texas rangeland.

PHOTORESPIRATION

Mooney and others (1977) measured photosynthetic capacity as high as $62 \text{ mg dm}^{-2} \text{ hr}^{-1}$ in honey mesquite under unlimited light, nutrient and water conditions at intercellular CO_2 pressure of $250 \mu\text{bar}$. However, nobody has measured such a high photosynthetic rate in the field because the field condition is far from optimum. In a hot summer, net photosynthesis of mesquite is substantially reduced. Water stress and high leaf temperatures are believed to cause this sharp decline in net photosynthesis since they accelerate photorespiratory CO_2 evolution. In normal conditions, most C_3 plants have photorespiration rates of 30 to 40% of net photosynthesis (Bjorkman 1966).

Photorespiration rate is determined as the difference between gross photosynthesis and net photosynthesis. Measured photorespiration in C_3 plants is sensitive to oxygen concentration and is virtually eliminated in an atmosphere of 2% oxygen at moderate temperatures (D'Aoust and Cavin 1972, 1974). Therefore, CO_2 exchange rate at 2% O_2 is an estimate of gross photosynthesis and net photosynthesis is the CO_2 exchange rate at 21% O_2 . By using the above method, we measured photorespiration rate in mesquite under field conditions.

In honey mesquite, a considerable amount of carbon (30% of net photosynthesis) is channelled into photorespiratory CO_2 oxidation cycle (PCO cycle). In late May, 1985 -- a dry period -- the daily maximum photosynthetic rate was $12.47 \text{ mg } CO_2 \text{ dm}^{-2} \text{ hr}^{-1}$, which approximates 1/3 of the rates obtained in the rainy period. Net photosynthesis reached a plateau at noon when the irradiance exceeded the light saturation requirement for mesquite. It then declined linearly as air temperature increased from 31.3 to $37.5^\circ C$. By 3:00 P.M. it was reduced to zero. In the meantime, photorespiration increased and reached a maximum. By 3:00 P.M., the rate of CO_2 uptake was equal to the rate of CO_2 evolution; i.e., CO_2 evolved through the photorespiratory CO_2 oxidation cycle was refixed in the photosynthetic CO_2 reduction cycle (fig. 4).

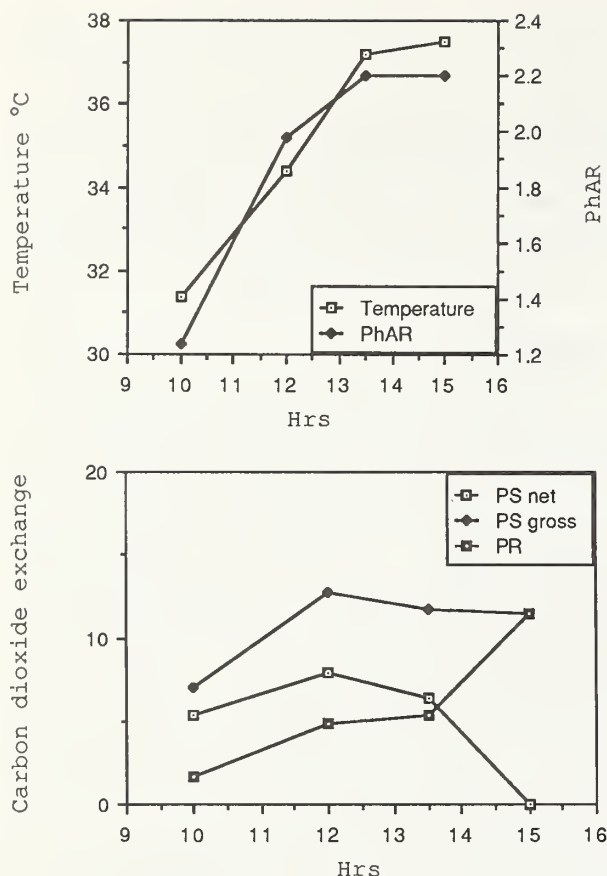


Figure 4--Upper: diurnal change in air temperature and photosynthetically active radiation (PhAR $\mu\text{mol m}^{-2} \text{s}^{-1}$). Lower: diurnal change in net and gross photosynthesis ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and photorespiration ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) as affected by air temperature.

Canvin (1982) has shown that at a temperature of 29.2°C , light intensity of $0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, and external CO_2 pressure of $340 \mu\text{bar}$, photorespiration rate of sunflower (*Helianthus annuus* L. var. CM90RR) was 45% of net photosynthesis ($14.22 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$). In mesquite, at leaf chamber temperature of 31.3°C , external CO_2 pressure of $320 \mu\text{bar}$ and photon flux density of $1.25 \mu\text{mol m}^{-2} \text{s}^{-1}$, the photorespiration rate was $2.7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, which was 30% of net photosynthesis. This photorespiration rate is very close to the range (3 to $10 \text{ mg dm}^{-2} \text{ hr}^{-1}$) reported by Zelitch (1971).

The photorespiration rate of mesquite is very responsive to temperature increase. At high temperatures, CO_2 solubility is more affected than that of O_2 , resulting in increased O_2/CO_2 ratio which inhibits rate of carboxylase reaction and enhances rate of oxygenase reaction. This detrimental effect of high temperature on net

photosynthesis of mesquite is more pronounced when soil water is limited, because insufficient latent heat transfer tends to raise leaf temperature even higher. Although mesquite has been described as productive in semiarid areas, it is doubtful that it can maintain high productivity in the summer months. Our data suggest that in midsummer honey mesquite only actively photosynthesizes in the morning hours, and becomes inactive in the afternoon.

The reduction in net photosynthesis has been attributed to decreased xylem water potential which triggers stomatal closure, hence increased resistance to CO_2 diffusion (Dye and Hanson 1978).

However, correlation between stomatal conductance and xylem water potential was not significant, and the conductance was more closely related to soil water status. Fig. 5 shows that when photosynthesis was high in the morning, xylem water potential declined to a low level, whereas zero net photosynthesis occurred when xylem water potential was higher.

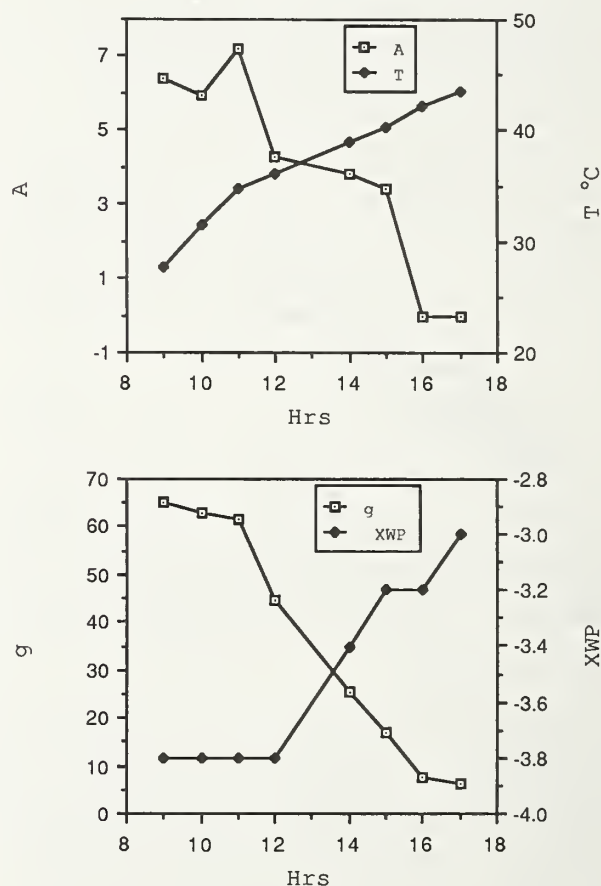


Figure 5--Upper: net photosynthesis (A, $\mu\text{mol m}^{-2} \text{s}^{-1}$) as affected by leaf temperature (T, $^\circ\text{C}$). Lower: diurnal changes in leaf conductance (g, $\text{mmol m}^{-2} \text{s}^{-1}$) and xylem water potential (XWP, Mpa) under a severe water stress conditions.

Increased resistance to CO_2 diffusion was unlikely to be the major limitation on photosynthesis

because the photosynthetic capacity is saturated at low intercellular CO_2 concentrations. It seems that the major influence of stomatal closure on photosynthesis of mesquite is through increasing leaf temperature which enhances the CO_2 compensation point and the O_2 inhibition of photosynthesis rather than through increasing resistance to CO_2 diffusion. As Fig. 5 shows, photosynthesis decreased with increasing leaf temperature.

Energetically, photorespiration is a wasteful process because ATP cost of the CO_2 assimilation is increased. In the hot dry summer, this may benefit the plant since extra heat can be dissipated through this process. According to the biochemical pathway, production of 1 mole CO_2 from PCO cycle consumes twice as much ATP and NADPH as its refixation in photosynthesis. It can also allow the plant avoidance of photo-oxidative damage to photosynthetic apparatus, such as chlorophyll bleaching.

CARBOHYDRATE TRANSLOCATION

It has been well known that food movement in the plant is from the site of photosynthesis to the site of growth or storage. Photoassimilate translocation follows the concentration gradient that becomes established between source and sink. This gradient is maintained osmotically by regulated loading of solutes into the sieve element companion cell symplast in source regions and regulated unloading in sink regions (Gifford and others 1984). The greater the utilization at a sink, the steeper the gradient. The gradient becomes greater when photosynthesis is more active. Therefore, photosynthesis, phenological development and environmental factors are the major considerations in the study of carbohydrate translocation in honey mesquite.

Unfortunately, most studies in the past have only focused on the relationship between sugar translocation and environmental factors, and overlooked the food producing process -- photosynthesis. The major emphasis has been devoted to sugar translocation to the roots, since this process is involved in herbicidal control of the plant. Carbohydrate translocation in the plant is driven by carbohydrate concentration gradient between the source and sink. Thus, a better understanding in carbohydrate translocation relies on our knowledge in the changing relations between source and sink as well as interactions among various sinks and source.

Root TNC trends of mesquite have been well established (Wilson and others 1975, Fick and Sosebee 1981, Seipp 1982, Dahl and Sosebee 1984). After reproductive growth is complete in the fall, more photoassimilate is available for downward translocation; in addition, the initiation and development of new crown buds and root growth also call for food importation, so downward carbohydrate translocation is operating at its maximum rate. A

peak root TNC is reached at the end of the growing season. Root TNC level in the early spring is somewhat reduced because of consumption by root respiration over winter. Immediately after budbreak, root TNC declines rather rapidly and drops to a minimum in May, about 42 days after budburst. This root TNC depletion is primarily caused by rapid root growth in the spring. In the subsequent period of about 20 days, root TNC is replenished and reaches a peak in mid June, which is often accompanied by flower abortion and initiation of small pods. This peak is followed by another sharp decline, and a minimum TNC occurs in early July; approximately 11 days is required for this discharge process. Pod elongation usually occurs during this period and is considered as a strong sink for photosynthates. Before summer drought starts, there is a second recharge period, which usually terminates about 84 days post budbreak. The third recharge event occurs during August through September and follows the major reproductive growth (fig. 6).

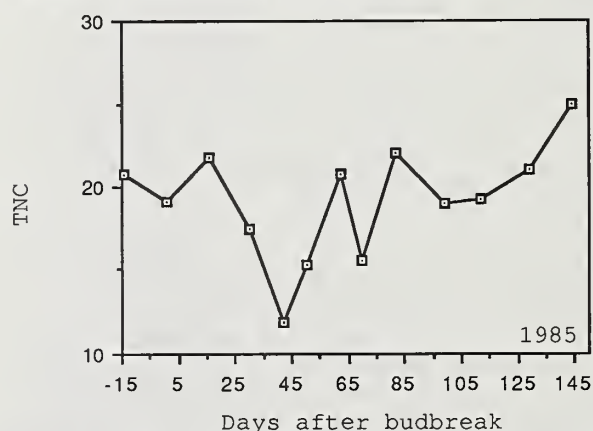


Figure 6--Root total nonstructural carbohydrate (TNC, mg/100mg) trend in honey mesquite growing on a sandy loam site in Lubbock, Texas.

Carbohydrate translocation to the roots is subjected to the effect of numerous physiological and environmental factors. The amount of carbohydrate being allocated to the roots depends on the development of other sink organs. Trees with a large proportion of flowers and pods would have lower root TNC concentration than trees with a smaller proportion of flowers and pods. Higher soil temperatures usually promote carbohydrate translocation to the roots, providing soil moisture is not limiting. In the spring, when soil has adequate moisture, soil temperature affects downward TNC translocation by stimulating rapid root growth, thus rapid TNC consumption. At low temperatures, the consumption of sugar is slowed due to reduced metabolic activity of roots and accumulation of TNC in the roots would tend to diminish the carbohydrate concentration gradient between the source and sink, and TNC translocation to the roots would be deferred. Furthermore, there is some evidence that low soil temperatures affect photosynthetic capacity of mesquite, which brings about a reduced source strength. Therefore, at low soil temperature both sink (root) strength and source strength would be reduced. We have found that on a sandy loam site where soil temperature is higher than on a clay loam site in

the spring, carbohydrate translocation to the roots is faster.

Soil moisture affects downward carbohydrate translocation through direct or indirect influence on plant physiological processes. The greatest influence is reduced photosynthesis under water stress conditions. When mesquite is severely water stressed, downward sugar translocation is slowed to a minimum or even stopped. Root activity is also affected by soil water deficit; therefore there is a diminishing requirement for influx of sugar. When the loading of sucrose at source sites becomes sluggish due to decreased assimilation rates and unloading at sink sites is blocked through reduced root growth, the driving force for the downward TNC translocation will no longer exist.

In a wet year, root TNC recharge would occur three times, whereas in a dry year, the roots can only replenish their reserve twice (Seipp 1982). The active downward carbohydrate translocation is a reflection of the overall high physiological activity of the plant. Seipp (1982) found that rapid increase of root TNC in early June, 1980, was related to higher than average soil water content in the rooting zone just prior to that period. Our results have shown that downward carbohydrate translocation was not affected by -1.5 MPa soil water potential.

The optimum condition for downward carbohydrate translocation has to meet both moisture and temperature requirements, but too much water in the profile tends to lower soil temperature. On a heavy soil, the greatest root TNC recharge occurs not during a period of saturated soil moisture condition, but during a period of higher soil temperature and relatively good moisture conditions. This seems logical because root growth is less sensitive to a moderate water stress than shoot growth (Bradford and Hsiao 1982). When a stress level is just enough to inhibit leaf expansion and reproductive growth, root activity may not be affected and can continue to serve as a strong sink for photosynthates. It has been generally agreed that the plant growing on a less mesic site would have an increased ratio of root to shoot biomass. Some controversies have been evoked on the effect of water stress on carbon translocation in the plants. Fick (1978) found that soil moisture at the 15-cm depth was negatively correlated with root TNC of mesquite ($r = 0.96$) during the phenological stages of green spikes and green pods. Wardlaw (1967) suggested that the velocity of translocation was little affected by water stress. As far as drought effect on carbohydrate translocation is concerned, it is necessary to define the stress level and the stress effect on related physiological activity of the plant. The question to be addressed is not whether water stress affects carbohydrate translocation, but how translocation is affected by different levels of water stress. Dahl and others (1971) and Sosebee and others (1973) found that water deficit in the surface soil was negatively correlated with root kill of mesquite by herbicide application. This does not mean that drier the soil, greater the downward sugar translocation. Dahl and Sosebee (1984) pointed out that dry

springs usually will not stress mesquite unduly, since deep moisture is generally available.

TNC concentrations in buds, stems and twigs are usually lower than those of roots and trunk (Fick and Sosebee 1980, Seipp 1982), suggesting the roots and trunk are more important storage organs. Since buds, stems and twigs are actively growing tissues, their reserves are likely to be consumed rather quickly, especially in twigs which have the lowest TNC concentration in the season. At the time of budbreak, TNC concentration in all plant parts decreases. Because stems and twigs are proximal to the buds, they are assumed to provide more carbon and energy to the emerging buds than the roots and trunks. Seipp (1982) suggested that the primary energy source for budburst of honey mesquite is derived from aboveground storage organs such as buds, stems, and twigs.

Since root TNC is mainly consumed by root growth, its concentration usually undergoes great fluctuation in the spring when the roots are rapidly growing. Rate of root TNC recharge is considerably higher than that of aboveground plant parts (Seipp 1982). It appears that the root system is the strongest sink in the downward carbon flow. This may explain why the root TNC recharge rate is greater for the trees with fewer flowers and pods and lower for the trees with many flowers and pods. Competition for photoassimilates between root growth and reproductive growth is often in favor of the latter. Therefore, pod elongation and floral development have marked influence on root TNC levels. Wilson and others (1974, 1975) suggested that maturing pods are primarily responsible for a low root TNC level during July. It has also been shown that in mesquite, carbohydrate translocation to the roots and stems is more active following the termination of reproductive stage and the recharge in the storage organ is considerably slowed during flowering. Wilson and others (1975) revealed that root TNC recharge was influenced by relative proportion of reproductive organs and the rate of recharge would be slow in the trees with young and blooming spikes and fast in those with mature pods.

Fick and Sosebee (1981) found that between development of green flower spikes and small pods during June, TNC levels in stems and twigs increased substantially while pod TNC remained low.

Our data have shown a similar trend with root TNC. This rapid translocation coincides with the great photosynthetic activity of the plant in this period. During the recharge period, increase in root TNC is positively correlated with rate of photosynthesis on a sandy loam site ($r = 0.81$, $P = 0.01$). When the immature green pods start pod filling beginning in late July (fig. 7), the pod TNC level increased at a much higher rate than the increase in stem and basal buds (Fick and Sosebee 1981). Since pod filling is a critical stage in plant regeneration, the trees have to sacrifice other plant parts in order to supply the pods with sufficient quantity of assimilates. Top priority for the plant at this time is maturation of seed pods and the importance of downward carbohydrate translocation becomes secondary. After pods mature, which usually occurs in mid August, there

is a significant TNC recharge in roots and stems for storage; whereas TNC declines in basal buds, which is associated with a flush of new buds.

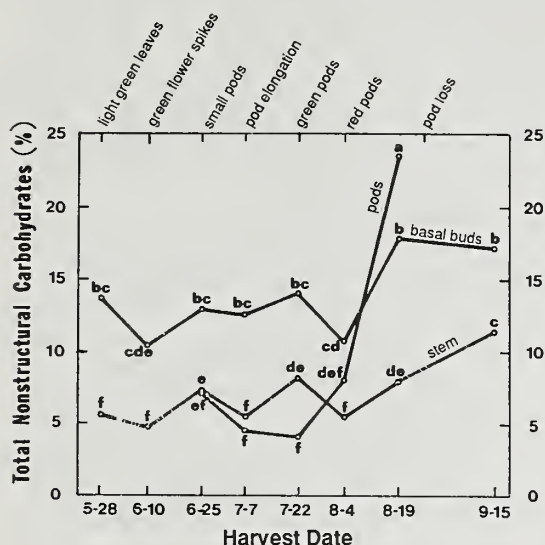


Figure 7--Total nonstructural carbohydrates in the basal buds, stems, and pods of honey mesquite trees harvested between May 28 and September 15, 1975. Phenological development is also indicated. TNC levels not followed by a similar letter differ significantly at the 5% level (Fick and Sosebee 1981).

Leaf TNC trend has received little attention in carbon translocation studies in honey mesquite. The leaf is the source of assimilate and leaf TNC level subjected to diurnal fluctuations, depending on rates of photosynthesis and translocation. Only limited information on leaf TNC is available at present. A moderate leaf TNC content occurred in mid June when the plants were actively photosynthesizing. This TNC level may reflect that higher rate of photosynthetic CO_2 fixation is

balanced by an active outward photosynthate translocation. Leaf TNC increased to a higher level in July when the plants were suffering water stress. The accumulation to TNC in leaves may be a result of reduced expansion growth and is probably related to osmotic adjustment of the plant since sugar is the major component of osmotica. It has been found that osmotic adjustment in honey mesquite could reach as high as 2.4 Mpa (Nilsen and others 1983), which is equivalent to a water potential of 1 molal glucose solution. This high TNC content has a great feedback inhibition on photosynthesis as indicated by much reduced photosynthetic rates in July. The feedback inhibition may involve a decreased concentration of metabolically available phosphate. The leaf TNC decreased in August, indicating that TNC was remobilized to mature pods. Even lower leaf TNC levels in October are probably due to rapid carbon translocation to roots and stems and symbolizes leaf senescence. More detailed information on leaf TNC content is needed in studying photosynthetic performance and translocation pattern of honey mesquite.

GROWTH REGULATORS

Much research has been conducted on hormones and growth regulators, but limited work has been done relative to honey mesquite. It was found that effectiveness of herbicide application to control mesquite was enhanced by addition of niacin, thiamine, biotin, or pyridoxin (Sosebee 1974). It was concluded that these vitamins stimulated root growth and improved effectiveness of herbicide. Brumley (1974) found that mesquite seedlings grown in soil temperature of 27°C had significantly higher niacin concentration in the roots than either those grown at 21°C or those grown at 32°C, indicating that 27°C is the optimum soil temperature for root growth of mesquite. The results have also revealed that low or high soil temperatures affect niacin translocation from the shoots to the roots. This is consistent with the carbohydrate translocation trend as influenced by soil temperature regimes. Since niacin is an electron acceptor in the respiration process, it is reasonable that its translocation follows the same pattern as carbohydrate translocation. On a heavy clay loam soil where lower than optimum soil temperature prevails in the spring, the highest photosynthetic rates were obtained at a soil temperature of 27°C. It is not surprising that transpiration and growth of mesquite reached maximum at the same temperature range. Higher niacin concentration stimulated shoot growth more than root growth at 27°C soil temperature regime than at either 21°C or 32°C temperatures. Therefore, the shoot/root ratio was higher in the trees with a higher niacin concentration as suggested by Brumley (1974). He also found that nodulated mesquite trees exhibited a tendency toward decreased shoot/root ratio and increased niacin concentration in the roots. When nodulated, more niacin is required in enhanced root respiration.

Thiamine is another important vitamin involved in carbon metabolism. Brumley (1978) found that as mesquite leaves became mature there was a steady increase in thiamine concentration. In the white flower stage, the major peak of thiamine concentration occurred in twigs and phloem, indicating a high metabolic activity in twig and flower and rapid translocation of thiamine throughout the plant. In the flower abortion stage, there were peaks in thiamine concentration in the phloem and roots, which coincided with root TNC recharge. During pod maturation, peaks in thiamine concentration occurred in all plant parts, suggesting an intensive biochemical synthesis and growth in both above- and belowground plant parts.

Thiamin and niacin concentrations were drastically reduced when soil water deficit occurred and thiamin concentration was less affected by soil temperature below 27°C (Brumley 1978). Thiamin and niacin concentrations were more associated with phenological development than edaphic factors. It appears that physiological activities of mesquite are regulated by the concentration changes in these vitamins, which are coupled with development stages and affected by the environmental parameters.

Ethylene is a natural product of plant metabolism, which can exert various regulatory control over plant growth and development and is recognized as a plant hormone. Parsons and Sosebee (1974) studied the effect of ethrel (an ethylene releasing compound) on the phenological development in honey mesquite. Their results revealed that bud potential of mesquite was not regulated by ethrel application. The bud number and development of the leaves following budbreak exhibited no difference between control plants and those treated with ethrel. However, the flower index increased following applying ethrel. The same stimulating effect on flowering was found in pineapples by Burg and Burg (1966).

Almost all physiological processes of honey mesquite are affected by soil conditions. For example, photosynthesis and conductance are highly correlated with soil moisture. Rate of transpiration is influenced by soil temperature (Wendt and others 1967). Mesquite cannot survive flooding and its growth is eliminated along the flood plains (Marks 1950, Busby 1970). Downward translocation of vitamins and carbohydrates is affected by both soil moisture and soil temperature. All of these seem to imply an existence of a communication between root and shoot. This communication must be mediated by a hormone produced in the roots. This hormone is probably cytokinins. Since cytokinins are synthesized primarily in root meristems, any factors affecting root meristematic activity may have profound effects on cytokinin synthesis. Cytokinins are known to promote protein synthesis and photosynthesis and stimulate stomatal opening (Meidner 1967, Jewer and Incoll 1980). When plants were water stressed, their roots contained much less cytokinin activity than the control plants and the cytokinin concentration in both roots and leaves were reduced by half (Itai and Vaadra 1968, 1971). Reduction in photosynthesis and leaf conductance of mesquite may be caused by a reduced cytokinin synthesis and transport from the roots to the shoots or as a result of decreased ratio between cytokinins and abscisic acid (ABA) - the stress hormone (Schulze 1986). It seems that response of honey mesquite to water stress or low temperature stress is primarily sensed in the soil by the root system. Root-shoot communication is involved in the stress response of the plant, which is probably mediated by hormones.

CONCLUSIONS

Plant ecophysiology is an exciting field. It is not a new concept, but it has received more emphasis during the last 30 years than ever before. Physiological studies help explain ecological relationships within natural ecosystems. Honey mesquite was selected as a case study for this presentation because of the amount of research that has been conducted on it and because of the familiarity of the authors with this species. Intentions of the data presented are not to suggest that all species respond physiologically to the environment the same as honey mesquite. But, it is suggested that plants growing in their native habitats are very well adapted and often respond to the environment differently than we perceive their response.

Seed polymorphism has evolved through natural selection to insure germination and seedling survival. Since the seedling stage of most, if not all, plants is the most vulnerable, it is important that seeds "land" in safe sites where their requirements for germination and subsequent seedling establishment can be met. Conditions conducive for germination and establishment do not occur every year. Therefore, germination of seeds and establishment of seedlings occurs at irregular and, perhaps infrequent, intervals which gives rise to erratic changes in succession and revegetation of deteriorated communities, particularly in the West and Southwest.

Basic physiological and morphological studies reveal that endemic plants are well-adapted to their habitats. Photosynthesis and transpiration are well tuned to take advantage of and to cope with prevailing environmental conditions. Generally, consumptive water use by endemic species is not as great as purported, except for phreatophytes. Photosynthesis also varies from laboratory and greenhouse studies. Plants adapted to high temperature regimes have high thermal stability and are very tolerant of the high temperatures.

More ecological studies should be approached from an ecophysiological viewpoint. Close attention should be paid to phenological development and to the different stages of growth. Environmental conditions should be evaluated in detail. Basic physiological measurements need to be repeated through time to ascertain variations associated with changes in environment and phenological development. A thorough understanding of the ecophysiological processes of both native and introduced plants will help improve management of these species and the communities they inhabit.

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WILDLAND SHRUB DIEOFFS IN UTAH: AN APPROACH TO UNDERSTANDING THE CAUSE //

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ABSTRACT: A survey of the 1984-1985 shrub dieoff in eastern and central Utah showed 734,500 acres of rangeland to be affected. Additional unsurveyed dieoffs occurred in western Utah valleys. Shrub species affected include shadscale, fourwing saltbush, budsage, winterfat, horsebrush, narrowleaf low rabbitbrush, and others. Although earlier dieoffs have been associated with severe drought, the recent dieoff was associated with a record high precipitation period. Possible interacting factors discussed include overgrazing, winter injury, drought, salinity-anaerobiosis, insects, disease, and host genetics. Information from the literature on these factors, the nature of past shrub dieoffs reported, and environmental factors coincident with the recent high precipitation period (1977-1986) are considered in formulating an approach to understanding the cause.

BACKGROUND

Utah range resource managers, including those of the Bureau of Land Management, U.S. Department of Interior, Utah Division of Wildlife Resources and Utah Department of Agriculture; range scientists from Utah State University, Brigham Young University, and Forest Service, U.S. Department of Agriculture; as well as ranchers and other private land owners, have registered concern and interest in a recent widespread loss of wildland range shrubs. The Bureau of Land Management (BLM) estimated that 1 million acres (Boyer 1986) have been affected in Utah alone. Other Great Basin States, Nevada and Idaho, have shrub populations that are also affected. Conditions of low vigor, decline, and mortality have been noted primarily in shadscale (*Atriplex confertifolia*), but also among fourwing saltbush (*Atriplex canescens*), big

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sagebrush (*Artemisia tridentata* ssp. *tridentata* and *A. t.* ssp. *wyomingensis*), budsage (*A. spinescens*), black sagebrush (*A. nova*), winterfat (*Ceratoides lanata*), greasewood (*Sarcobatus vermiculatus*), horsebrush (*Tetradymia spinosa*), spiny hopsage (*Grayia spinosa*), bitterbrush (*Purshia tridentata*), and narrowleaf low rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus* var. *stenophyllus*). This immense "dieoff" (unexplained partial to complete death of shrubs on sites up to hundreds of acres or more) occurred in the later portion of an historically record high-precipitation period between 1977 to 1986 (see section on drought and figure 1). Because the plant species affected include shrubs important for forage and habitat on the 40 million acres of salt desert extending across the Great Basin and northern Colorado Plateau (Holmgren and Hutchings 1972; Hutchings and Stewart 1953) this large-scale shrub dieoff is of importance to wild and domestic ungulate and other wildlife interests.

Of more intrinsic importance are the ecological implications in the shadscale zone. Because these phenomena have been little studied, the nature and direction of plant succession in dieoff areas is not well understood. For the shadscale zone, successional unknowns are posed by the presence of exotic annual plants such as cheatgrass (*Bromus tectorum*), halogeton (*Halogeton glomeratus*), Russian thistle (*Salsola iberica*), tansy mustard (*Descurainia sophia*), summercypress (*Kochia scoparia*) and others. Disturbed sagebrush-grass vegetation on the Snake River Plains of south central Idaho succeeds through a series of annuals (Piemeisel 1951) terminating often in a cheatgrass climax that is perpetuated to some extent by range wildfire. Cheatgrass flourished as shadscale declined during the recent high moisture period. Because few of the major shrubs of the shadscale zone sprout following fire, widespread wildfire could have the potential for converting cold desert shrublands to annual herb communities. This would also increase the danger of fires spreading to adjacent sagebrush-grass and pinyon-juniper zones.

Eighty-three percent of the western United States is covered with forest-range vegetation (USDA Forest Service, Forest-Range Task Force 1972). Of this, 51 percent is dominated by shrubs, constituting an estimated 820 million acres (Plummer 1974). Shrubs are also a component of grasslands, and in forests shrubs occupy open spaces and understory. Thus, the western United States is predominately an arid to semiarid

shrubland habitat, one that has evolved in response to interacting combinations of drought, poor soil aeration, low soil mineral nutrients, shade, fire, and winter cold (Stebbins 1975). Aside from more utilitarian values (animal forage, recreation lands, firewood, medicinals, biomass raw materials), this immense shrubland system provides watershed, influences air quality and climate, and supports numerous animal life forms. Understanding the biology of this system is an unavoidable fundamental that is urgently in need of study.

THE RECENT SHRUB DIEOFF

Dieoff Survey

A partial BLM survey (USDI-BLM 1985-1986) of the Utah shrub dieoff by range conservationists in the Moab, Richfield, and Vernal Districts showed 734,500 acres affected in four shrub-dominated communities as follows: black sagebrush 8,000, big sagebrush 16,000, fourwing saltbush 20,500 and shadscale 690,000 acres. Where fourwing saltbush was the dominant shrub, shadscale was a common associate. Where shadscale was dominant, community composition ranged from almost pure stands of that species to associations in which fourwing saltbush, budsage, winterfat, hopsage, horsebrush, low rabbitbrush, and other species were subdominants. Mortality ranged from 10 to almost 40 percent in fourwing saltbush stands. Mortality percentages were higher (20-95 percent) in shadscale communities.

In western Utah (not included in the survey), entire shadscale populations died on many valley bottoms, on slight rises, and in upland depressions. On peripheral valley slopes, only scattered dead and dying plants were more typical. Scattered dead and dying plants were also typical of all other shrub species affected.

Utah Division of Wildlife Resources (Stevens 1985) reported spotty to extensive areas of dieoff or low vigor of big sagebrushes, mountain rubber rabbitbrush (Chrysothamnus nauseosus ssp. salicifolius), bitterbrush, and Atriplex spp. in areas located more in the mountain shrub zone. Bitterbrush and big sagebrush mortality was found over several hundred acres in what appeared to be a rather distinct elevational belt, along the east side of Skull Valley, Tooele County, UT.

Nature of Dieoff

The most widespread mortality of shrubs was reported to have occurred in the summers of 1984 and 1985. Partially dead shrubs have continued to decline and die. Insect damage and disease were most frequently judged to be the cause of death with occasional mention of drought, winterkill, or high water table. Intensity of large animal use (primarily deer), for the most part, was considered a factor only with Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) decline, especially in the Browns Park area of the Vernal BLM District. As of spring 1986 there

appeared to be little or no regeneration in most areas of extensive shrub mortality or decline. Native perennial grasses, cheatgrass, and other weedy annuals have flourished in dieoff areas. Among the big sagebrushes, especially Wyoming big sagebrush, affected stands showed symptoms of low vigor and slow decline, not mass death. Decline symptoms included slow growth, low seed production, shoot dieback, and occasional death of the entire plant. With the Atriplex spp., there was not an obvious relationship between age or size and plant death. Fourwing saltbush dieoff affected populations had low vigor, severe basal decay, rootlet mortality, and root borer activity in decayed tissue and heart wood. In some areas heavy animal use was also evident.

In the shadscale zone, shrub mortality, especially of Atriplex confertifolia, occurred as mass dieoffs. Death of entire populations occurred over hundreds of acres. Dying, as well as apparently healthy, plants in dieoff zones typically had severe fine rootlet mortality and active rot and decay in larger roots. Shoot dieback was commonly associated with death of the corresponding portion of a plant root system. In valley bottoms, mid-valley rises, and upland depressions, death of entire populations occurred during a short period, perhaps 1 to 2 years. At higher elevations, and on peripheral valley slopes and hills, dieoff was characteristically a scattered slow-decline and death that continues to the present. There were, however, shadscale populations even on valley bottoms and adjacent to dieoff areas that were little if at all affected. Dieoff among associated shrubs (such as budsage, winterfat, narrowleaf low rabbitbrush, and horsebrush), particularly in western Utah valleys, usually involved a slow decline rather than mass deaths. Mortality of small rootlets, rot of larger roots, and shoot dieback were also associated with these species.

Other than grasshopper damage (covered in a later section), no large-scale epidemic of defoliating insects has been associated with any shrub species involved in the recent dieoff. Mealybugs were common on shadscale in some areas and appear to be widespread in the Great Basin and adjacent areas. When infestations were found, they were usually either on lower stems protected by duff or living portions of the upper fractured tap root below the soil surface. Occasionally root-borer insect larvae were found in decayed heartwood tissues of shadscale roots.

Mass shadscale dieoff occurred on diverse sites and soil types. In western Utah, dieoff occurred on the heavy silty-clay soils of valley bottoms, sandy-clay soils of mid-valley rises, and gravelly soils of alluvial fans. In the Grand River Valley area of the Colorado Plateau in east-central Utah, extensive shadscale dieoff occurred on gravelly to sandy soils derived from Book Cliff alluvium.

CAUSE OF SHRUB DIEOFF

The purpose of this section is to discuss the following environmental factors as possible

causes of extensive shrub dieoff: large animal use, winter injury, drought, soil salinity, anaerobiosis, insect epidemics, and plant disease. Throughout, emphasis is on the Chenopodiaceae (most specifically shadscale) because it was the most severely affected by dieoff. Therefore, the interacting role of Atriplex genetics, evolution, and distribution is an important consideration. Rather than basing this discussion on an exhaustive review of original research, syntheses of reviewers of various subjects will be used where available. For each potential causal factor, the nature of the mechanism of plant injury will be briefly described as a basis for comparing relevant information in the literature to mortality of wildland shrub species of interest. Then, using the preceding largely subjective description and assessment of the recent shrub dieoff, each environmental factor will be evaluated as to its possible role in the dieoff.

Large Animal Use

There are many reports of shrub mortality resulting from domestic and big game animal use (Frischknecht and Harris 1973; McArthur and others 1988; Stewart and others 1940). Range scientists have long studied the influence of animal feeding on plant productivity and vigor, and on community composition and succession (Ellison 1959, 1960). In the shadscale zone, browsing by livestock tends to favor shadscale (Holmgren and Hutchings 1972). This response is less related to its innate palatability than to its spiny nature. If animal feeding causes decline and death of specific shrub species and alters community composition, the decline occurs over extended periods of time except when use is extreme (Blaisdell and Holmgren 1984). Long-term controlled studies on the influence of browsing can be confused by shorter term, overriding, events such as drought and insect epidemics (Holmgren and Hutchings 1972; West 1982). When large-scale death and decline of shrubs is caused by overgrazing it is clearly restricted to the area of overuse.

Large animal use did not appear to be a factor in the recent shrub dieoffs, except as a possible intensifying or predisposing factor (perhaps in such recent cases as fourwing saltbush decline in San Juan County, UT, and Wyoming big sagebrush decline at Browns Park in Daggett County, UT). The extensive areas of shadscale dieoff did not appear to be correlated with intensive livestock use.

Winter Injury

Winter injury has been implicated as a cause of mass shrub dieoff in the intermountain West. Unseasonal high precipitation periods or overland flow of water from high-intensity summer storms could possibly predispose plants to winter injury or drought. Death of shrubs over large areas has been observed following overland water flows at the Forest Service Desert Experimental Range and elsewhere in west-central Utah by Ralph C. Holmgren (Forest Service) and Kimball T. Harper

(Brigham Young University). If plants remain at least partially submerged for extended periods, death could result from oxygen-deficient root systems. However, overland water flow late in the season can stimulate abundant new shoot growth. This succulent growth may not reach sufficient winter dormancy in time for winter freezing or drought hardiness in time to adjust top growth to water deficits during the following summer's dryness.

Cottam (1937) reported extensive damage to several shrub species of the Sonoran zone in southwestern Utah following an unusual cold period. In a survey report of Nelson and Tiernan (1983), damage was reported for 36 shrub species following the unusually low precipitation winter of 1976-1977 in the western United States. In the mountain-shrub zone Ceanothus, Arctostaphylos, Juniperus, Artemisia, and others were most likely killed or damaged by winter injury while low-elevation cold-desert shrubs such as Atriplex, Ceratoides, Grayia, Sarcobatus, and others were likely damaged by drought alone. Almost complete winter-kill of mountain big sagebrush stands (Artemisia tridentata ssp. vaseyana) occurred on an estimated 138,000 acres while partial kill occurred in many other areas. Other reports of winterkill or injury include bitterbrush (Jensen and Urness 1979; Smith and others 1965), fourwing saltbush (Van Epps 1975), and Ceanothus (Stickney 1965).

Winter injury is a rather broadly encompassing term and its mechanisms are diverse. Plants receive winter injury by freezing because of insufficient cold-hardiness, or in cold-tolerant plants, from the lack of winter dormancy. Winter injury can also be caused by desiccation resulting from transpiration when the root system is frozen, or the soil is frozen or too dry for supply of needed water. The most critical periods are usually in early or late winter. With winterkill dieoffs, a fairly reliable diagnosis can be based on the uniqueness of symptoms and coincident climatic episodes.

Studies on the 1976-1977 mountain big sagebrush winterloss in southwestern Idaho at the Reynolds Creek Experimental Watershed (Hanson and others 1982; Schumaker and others 1979) supplied experimental evidence to support winter injury as the cause. Mortality was near 100 percent where sagebrush plants were normally covered by deep snow and slight in areas of normally shallow cover. Below average soil moisture and frozen soil during periods when temperatures were high enough for plant respiration and transpiration implicated physiological drought as the cause of winter kill.

Apparently no similar large-scale winter injury event occurred during 1977-1986, a period of high precipitation and heavy winter snow cover. However, winterkill from freezing of nondormant plants could account for the death of big sagebrush and bitterbrush along an elevational belt on the east face of Skull Valley in Tooele County, UT, in the spring of 1985.

Drought

Although the severe overgrazing-caused deterioration of grass on intermountain rangelands during the early 1930's was the focus of attention, the first notice of shrub dieoff came with the drought of 1934, the culmination of a 14-year dry spell. On the upper Snake River Plains of southeastern Idaho, Pechanec and others (1937), studying the effects of the 1934 drought on the sagebrush-grass type, found a 46.8 percent reduction in cover of all shrubs relative to the 1932 cover: *Artemisia tripartita* 48.7, *Chrysothamnus puberulus* 29.1, *Purshia tridentata* 49.1, and *Tetradymia canescens* ssp. *inermis* 48.8 percent. In the shadscale zone of the Great Basin, episodic dieoffs of shadscale and associated shrubs have been observed over the years and the cause was usually attributed to drought. Stewart (1935) observed a general mortality of forage plants of "appreciable magnitude" on the winter ranges of Utah and Nevada during the 1931-1934 drought period. At the Desert Experimental Range, he reported a general mortality of 20 percent for shadscale and white sage (winterfat). Mortality reached 60 percent in heavily grazed areas. Little rabbitbrush mortality was apparently less, judged so by Stewart because of less grazing pressure resulting from lower palatability. Also at the Desert Experimental Range during the drought periods of 1933-1934 and 1942-1943 Hutchings and Stewart (1953) and Hutchings (1954) referred to a widespread shadscale mortality of 20-30 percent, while black sagebrush, budsage, and winterfat had little mortality. Ellison (1959) called attention to drought as an environmental factor in plant succession citing an apparent drought-caused dieoff of little rabbitbrush at the Desert Experimental Range in 1952. A combination of drought, competition, and moderate grazing tended to favor *Artemisia nova* (black sagebrush) over little rabbitbrush. His study site was a nonsaline bajada on the west side of Antelope Valley where shadscale does not occur. However shadscale dieoff could have occurred on the heavy soils of valley bottoms because in other reports shadscale is considered to be less drought tolerant than little rabbitbrush. Insect damage has also been suspected as a factor in reduction of little rabbitbrush (Holmgren and Hutchings 1972).

Following the severe drought of 1958-1961, Holmgren (1963) studied the effects of drought in the shadscale and sagebrush zones of western Nevada in the Carson Desert area. He sampled 23 locations in a 50- by 150-mile area for shrub death and cover reduction on different sites and soil types. With all species on every site there was a reduction in cover. On the various sites, total cover reduction ranged from 20 to 75 percent. With some shrub species the extent of death was influenced by soil and site: budsage mortality was generally less than 10 percent in the sagebrush zone, but complete in the sandy soils of the upper shadscale zone; smooth horsebrush (*Tetradymia glabrata*) in the shadscale zone died out completely on shallow dune sands that were overlying lacustrine silt-clays, but

only 30 percent death occurred on sites with deep sand. Mortality of shadscale and little greasewood (*Sarcobatus baileyi*) was about 20 percent regardless of site. Other shrubs (winterfat, fourwing saltbush, spiny hopsage, big sagebrush, and Nevada jointfir (*Ephedra nevadensis*) had light mortality. Thus, with this drought, in the shadscale zone of western Nevada, there tended to be a shift in shrub species composition from budsage and horsebrush to hopsage, winterfat, and jointfir, with some reduction in shadscale.

During the 1958-1961 drought, shadscale dieoff was also extensive at the Desert Experimental Range (Holmgren 1988). Similar dieoffs of shadscale were observed there in the drought of 1971-1972 and 1976-1977 (Blaisdell and Holmgren 1984). Holmgren and Hutchings (1972) concluded that many shadscale plants "die when one dry year follows directly upon another." Shrub dieoff in the shadscale zone, although regularly associated with drought periods, has not been studied in detail except for the Holmgren (1963) study. There is no experimental evidence for concluding a droughtkill, cause-and-effect relationship based on an established water-deficit death-point.

There are, however convincing leads based on a comparison of weather records and observed dieoffs. A review of annual precipitation over a 50-year period at the Desert Experimental Range and observed shadscale dieoffs supports the Holmgren-Hutchings (1972) rule (fig. 1). When annual precipitation was 1.0 or more inches below the 50-year average (6.29 inches) or 4.5 inches or less for 2 consecutive years, noticeable shadscale dieoffs usually occurred. During this period the only 2-year drought period of apparent exception was 1955-1956. This was part of an 11-year dry spell (1948-1959) that terminated with the dieoff of 1958-1961 (Holmgren 1963). Shadscale dieoff probably occurred in 1952-1953 based on the notice of little rabbitbrush drought-kill of that time (Ellison 1959). A mass dieoff at this time could have masked the potential 1955-1956 episode because of insufficient time for shadscale regeneration. The record of shadscale dieoffs is sketchy; perhaps because dieoffs were common and because the assumption that droughts caused the dieoffs was apparently well accepted by 1954 (Hutchings 1954, p. 14), some mass dieoffs could have gone unreported at that time. Interpretation of biological phenomena, relevant to annual precipitation on a water-year basis (October through September) has the uncertainty of timing. Heavy precipitation during the last week in September for example would have little biological effect for that amount in that year but could be considerable for the following year.

During the period 1977-1984 (with a 1-year exception, 1982-1983) well above average precipitation occurred. This was the longest sustained wet period in the 50-year history of the Desert Experimental Range. The mass shadscale dieoff that occurred in 1983-1985 in the absence of drought was observed in many areas of the Great Basin shadscale zone. This

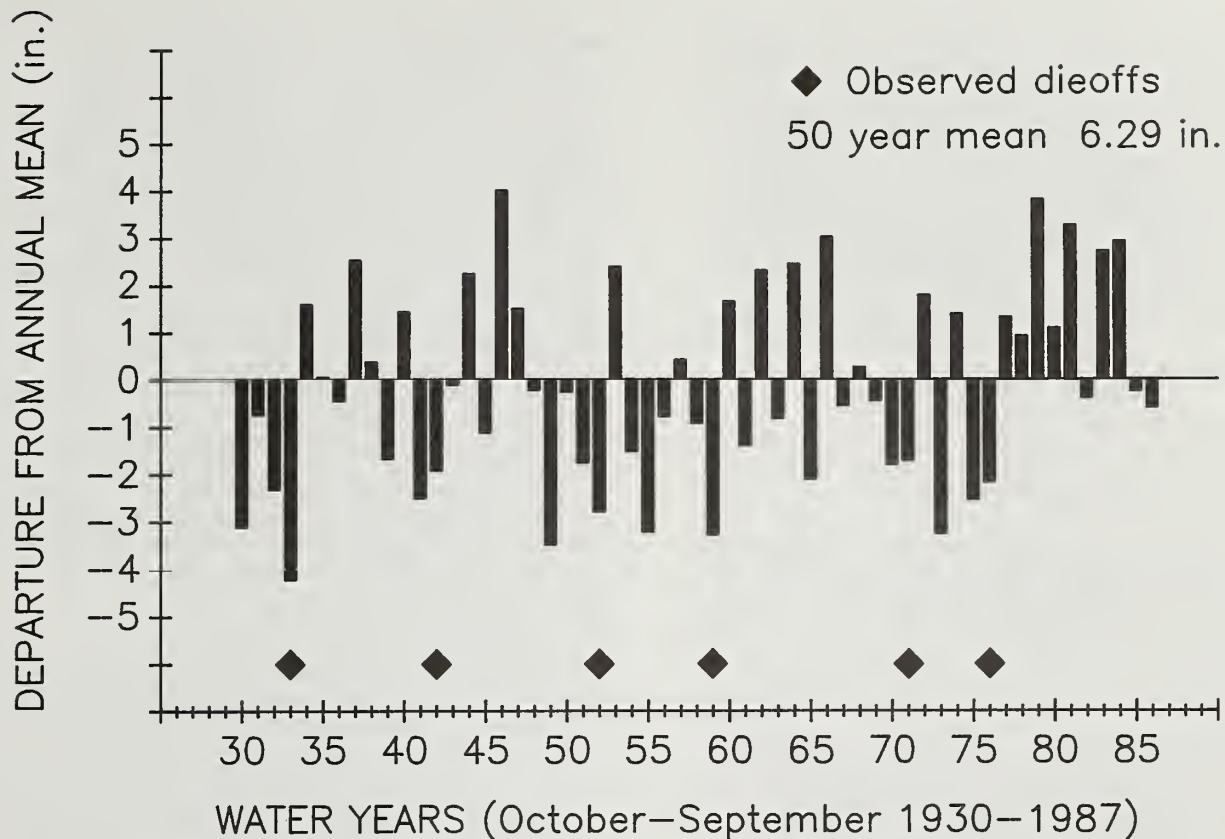


Figure 1--Association of observed shadscale dieoffs with drought periods at the Desert Experimental Range. Amounts prior to 1934–1935 were extrapolated from Deseret, Utah (74 miles distance) weather records and after 1983–1984 from Wah Wah Ranch (14 miles distance).

was the only major shadscale dieoff of record that was not associated with drought. Unfortunately no weather records or observations on shrub dieoff have been made at the Desert Experimental Range after 1983–1984.

A Sketch of Great Basin Physiography, Climate, and Vegetation

The following sketch of Great Basin habitat is intended as a background for consideration of soil salinity and anaerobiosis as potential causes or predisposing factors of mass shrub dieoff.

The north-south oriented basins and mountain ranges that comprise the Great Basin formed during the Rocky Mountain uplift. With the continued rise of the Sierra Nevada during the Pleistocene and the consequent climatic aridity of Great Basin country, outward precipitation drainage to the ocean was slowly terminated. As a consequence, vegetation changed from more mesic forests, woodlands, and grasslands to dominance of drought-tolerant shrubs (Axelrod 1950; Axelrod and Ting 1960), the evolution of which still continues. Great Basin valleys are filled to varying degrees with outwash of the sedimentary deposits of ancient inland seas that raised during formation of present bordering mountain ranges. Peripheral valley alluvial slopes or

bajada composed of coarse gravelly soil at their upper limits gradually change to more gravelly sandy, then loamy soils at their lower reaches. Pleistocene lakes filled numerous Great Basin valleys; with their disappearance, sedimentary lake deposits developed into the silty to heavy clay soils presently found. The larger valleys or basins may therefore have large expanses of very uniform soil.

The hydrologic cycle of the Great Basin is one of internal drainage and evaporation of precipitation coming as summer rain to valleys and mountains, and winter snows primarily to the mountains. Higher valleys, if not topographically closed, drain to lower basins. Thus, salts carried by snowmelt and intense summer storm runoff or groundwater movement accumulate in a declining gradient outward from the lowermost portions of closed valleys, or even perched, closed depressions at higher elevations. It is in these niches that the halophytic shrubs, primarily chenopods, have been and continue to be evolving.

Large fluctuations in amount of precipitation could result in the possible fluxing of water tables in certain valley bottoms, and in others the existence of ephemeral saline lakes or playas with evaporative surfaces. A somewhat banded, perplexing mosaic of vegetation radiates from

these salt playas and marshes. Species composition changes along an osmotically induced stress gradient (Branson and others 1967): from fungi, algae, pickleweed (*Allenrolfea occidentalis*), and alkali sacaton (*Sporobolus airoides*) (the salt marsh); through saltsage (*Atriplex tridentata*), greasewood, desert molly (*Kochia americana*), shadscale, winterfat, and budsage (the salt-desert-shrub or shadscale zone); to the big sagebrush and pinyon-juniper zones. Community distribution and composition of any given site is probably determined by species adaptation (by evolution) to tangled interactions of such factors as edaphic and climatic situations, interplant competition, and animal herbivory. Explanation of observed patterns remains somewhat puzzling (Billings 1949; Branson and others 1967; Gates and others 1956; Goodman 1973; Shantz 1925; Stewart and others 1940; West 1982; West and Ibrahim 1968).

For an enchanting account of the physiography, climate, and cold desert vegetation of the Great Basin see Holmgren (1984). Included are references to basic works on the subject.

Soil Salinity

There are an estimated 54.4 million acres (22 million ha) of saline soils in the 11 western States (McKell and others 1986). Naturally saline and sodic soils occur primarily in areas of semiarid climate and in closed drainage basins where soils are derived from shale, siltstone, and other sedimentary deposits of ancient inland salt-water seas. With insufficient precipitation for leaching or in closed drainage basins salts accumulate in the upper soil profile. The most common ions involved in saline soils are: Na^+ , Ca^{2+} , Mg^{2+} , Cl^- , SO_4^{2-} , HCO_3^- . Salts of these ions can form in various combinations and amounts. Soils are considered saline (adversely affecting most domestic plants) at an electrical conductivity of 4 mmho/cm at soil saturation, with the range of plant tolerance among plant species being at about half to twice this amount (Bernstein 1975).

Much of the present information on the effects of soil salinity in plants has come from agricultural crop experimentation; the processes for desert plants are not thought to be basically different (Caldwell 1974; Kleinkopf and others 1975; Wallace and others 1973). Different interacting environmental elements, however, require special further consideration in the assessment of salinity effects on desert plants (Caldwell 1974): low soil moisture, low atmospheric humidity, summer-winter temperature extremes, sporadic temperature and precipitation fluctuations, low available soil nitrogen.

Symptoms of adverse salinity in plants include slower growth, stunting, smaller more succulent leaves, darker green leaves, and leaf wilting. With woody plants, leaf tip-burn and necrosis commonly occur. At high salt concentrations (the thresholds of which are determined by specific plant adaptation, halophyte or nonhalophyte),

the limits of protective mechanisms are exceeded, membrane selectively is lost, and there is an influx of salt into the shoots with lethal results. The symptoms induced by adverse salinity result from an interaction of three general processes. First, failure of plants (halophytes and nonhalophytes) to compensate internal osmotic potential with an increased salinity-caused reduction in osmotic potential of the soil solution leads to a series of events: turgor reduction, water stress, stomatal closure, reduction in gas exchange and consequential reduction in transpiration, and reduced photosynthesis. Second, excess Na^+ and Cl^- accumulation, as well as excesses of other elements (boron, selenium, lithium), can cause toxicity and necrosis. Third, nutritional imbalances usually involving ratios also occur. Adjustments of plants to adverse salinity requires additional energy for osmotic regulation and maintenance respiration. Energy deficit is further complicated by reduced formation of energy-rich molecules (adenosine triphosphate, ATP) used in metabolism of available carbohydrates.

Various protective mechanisms for salt tolerance have evolved. Resistance to water deficits occurs by formation of fewer stomata, stomatal closure, increased leaf cuticle thickness, and root proliferation which increases the root-leaf surface ratio. Both nonhalophytes and halophytes (halophytes at a higher magnitude) actively accumulate electrolytes to maintain an osmotic gradient in the face of increasing soil salinity, to maintain turgor. Osmotic adjustment or regulation occurs by compartmentalization of salts in vacuoles that are balanced osmotically by nontoxic organic solutes in the cytoplasm. Tolerance to salt toxicity also occurs partially from these neutral cytoplasmic organic solutes through protection of root membranes and by selective translocation. Reduction of ion concentration occurs through increased shoot growth and leaf succulence, and by salt excretion through salt glands, such as the bladder trichomes of *Atriplex* (Lipschitz and Waisel 1982; Schirmer and Breckle 1982). Plants also isolate ions in old leaves, leaf petioles, tracheids, and roots.

These generalities on salinity symptoms and protective mechanisms in plants were derived from, and more specifics can be obtained from, various reviews and associated basic works on the subject (Bernstein 1975; Caldwell 1974; Flowers and others 1977; Greenway and Munns 1980; Pasternak 1987).

Great Basin habitats, especially old Lake Bonneville and Lahontan basins, certainly present the potential for fluctuations in soil salinity in response to fluctuations in precipitation. High and low precipitation extremes, either from soil drying (upward movement of salts by capillarity and lack of leaching) or soil moisture saturation (raised water tables) could result in increased salinity. Although there have been studies on shrubs and soil salinity in the Great Basin none have involved interaction with mass shrub dieoff. There are undocumented reports of mass shrub

dieoff in Australia when salts moved upward in the soil profile during extended drought periods. Increased soil salinity could be a factor in the drought-associated dieoffs of shadscale at the Desert Experimental Range referred to above. Studies on salt tolerance of shadscale zone vegetation in the Great Basin and adjacent areas have focused on seedling germination and growth (Chatterton and McKell 1969; Kleinkopf and others 1975; Richardson and McKell 1980; Springfield 1966; Workman and West 1969); and shrub distribution (Branson and others 1967; Gates and others 1956; Goodman 1973; Goodman and Caldwell 1971; Moore and others 1972). Extrapolation of this information as a clue to shrub dieoff is rather indirect, although the ordination of species by tolerance of mature plants to salinity or osmotic stress (increasing order of tolerance: big sagebrush, black sagebrush, budsage, winterfat, shadscale, desert molly, greasewood, saltsage, mat saltbush) (Branson and others 1967; Goodman 1973) proposes constructs for hypothesizing.

During the recent shrub dieoff in the upper shadscale zone where Wyoming big sagebrush and shadscale are intermixed, cases of severe shadscale dieoff occurred, whereas big sagebrush remained healthy; an event not likely to result from elevated soil salinity. Around the fringes of a rising Great Salt Lake where shadscale and saltsage intermix, shadscale died but saltsage remained healthy; an event likely to result from a level of salinity or anaerobiosis excessive for shadscale but not saltsage. The lethal salinity threshold for the various intermountain cold desert shrubs is not known.

Anaerobiosis

Prolonged full saturation of soil with water, severely reducing oxygen diffusion into the soil, leads to an anaerobic soil environment (waterlogging). Roots of plants as well as soil microorganisms must then contend with life at little or no soil oxygen (anaerobiosis). The recent above-average precipitation period (1977-1986) across the Great Basin and adjacent area could have resulted in instances of soil waterlogging or high soil moisture for extended periods. Prolonged high precipitation could result in raised water tables in certain basins or valleys. Intense rainfall or snowmelt could result in accumulation of water (resulting in soil waterlogging) on basin floors or depressions where impervious or semi-impervious soil strata slow drainage. A near tripling of the size of Malheur Lake in Oregon (Ganskopp 1986), the resurgence of Sevier Dry Lake and rapid rise of the Great Salt Lake in Utah are notable evidence of an unusually high precipitation period.

Damage from temporary or prolonged waterlogging of especially nontolerant plants (particularly accelerated at warm to high temperatures) is manifest by various symptoms (Drew and Lynch 1980). These include a slowing or cessation of root growth, senescence of older leaves, shoot wilting, leaf epinasty and abscission, and

eventual death of the entire plant. Waterlogging during cold weather causes little damage, probably because of the low rate of plant respiration. As further outlined by Drew and Lynch (1980) plant injury from anaerobiosis possibly results from four processes: 1) accumulations of toxins that form in anaerobic soil or roots, 2) lack of water uptake through damaged root membranes, 3) hormone imbalance resulting from malfunction of leaf and root metabolism and reduced translocation, and 4) mineral deficiency resulting from inhibited uptake and translocation or reduced amounts of nutrients available in the soil.

Following soil waterlogging, existing soil oxygen is used within a few minutes to hours by roots and soil microorganisms. In general, soil microorganisms can exist at a much lower soil oxygen level than roots of higher plants, thereby increasing the advantage of potentially pathogenic types. An early vital system thought to fail in the plant is the production of energy rich molecules (ATP) that drive metabolic systems (Givan 1968). In a short time (as a result of ATP deficit), the root cell membranes begin losing differential permeability and there is a greatly increased efflux of cytoplasmic metabolites into the soil (Hiatt and Lowe 1967). Dormant spores of certain fungi (including potential pathogens) are stimulated to germinate by these nutrients. Increased root exudation during plant oxygen-stress would tend to increase the zone of influence. Fungal germ tubes and mobile zoospores follow exudate-nutrient gradients to infect rootlets. If soil salinity is associated with waterlogging (a likely event at Great Basin salt desert sites) there would also be an increased influx of potentially toxic soil-water ions (Na^+ , Cl^-) (Barrett-Lennard 1986) that could further stress the plant and possibly accumulate to lethal amounts. A combined waterlogging-saline environment can either increase or decrease vulnerability of plants to infection by pathogenic organisms depending on the stress-state of the host plants, as well as favorability of the waterlogged environment to a specific pathogen. Activity of some fungi (watermolds or pythiaceus fungi) is enhanced by high soil-water matric potentials. However these fungi may also be inhibited by proliferation of anaerobic microbial antagonists under this environment.

To various degrees, plants, both waterlogging tolerant and nontolerant, make some adjustments for anaerobiosis. Physiological, metabolic, and anatomical adjustments occur that provide some tolerance or avoidance of oxygen deficiency (Drew and Lynch 1980). Responses that are evidently under hormonal control, initiated by anaerobiosis, cause a slowing of growth, a redistribution of mineral nutrients to young leaves and a closing of stomata which reduce both nutrient and water stress. Alternate metabolic pathways, particularly with waterlogging-tolerant species, impart some control over formation of the toxic end products of anaerobic respiration. Aerenchyma (tissue with specialized air channels) forms in newly developing adventitious roots and in existing stems by cell lysis. Aerenchyma

apparently enables increased movement of oxygen from shoots to roots (Drew and Lynch 1980).

There is little reported information on anaerobiosis as a factor in the shrub dieoffs of consideration here. Although some dieoff symptoms are similar to those discussed above for anaerobiosis, they are not easily distinguished from symptoms induced by drought, salinity, and vascular wilt diseases. Symptom induction by any of these factors could result from disruption of the same basic physiological processes (for example, maintenance of turgor). Relevant to anaerobiosis of desert shrubs is the general conclusion that big sagebrush is intolerant of poorly drained, fine-textured, highly moist soils (Branson 1956; Fosberg and Hironaka 1964; USDA Forest Service 1937; Vallentine 1980). Lunt and others (1973) gave experimental evidence in support of this. Big sagebrush and creosote bush required a relatively high oxygen diffusion rate (0.50 and 0.45 mg cm⁻² min⁻¹ respectively) compared to bursage (*Franseria dumosa*) at 0.30, a rate requirement more comparable to the generally high moisture tolerance of agricultural plants.

A study of shrub tolerance to inundation and high water tables around a rising Malheur Lake in Oregon during 1983-1984 (Ganskopp 1986) indicated Wyoming big sagebrush was most sensitive to high water levels followed by rabbitbrush (*Chrysothamnus viscidiflorus*) and greasewood. After 21 to 28 days inundation of big sagebrush, complete mortality occurred; many plants were also killed when the water table came within 6 to 10 cm of the soil surface. Decline and death of rabbitbrush and greasewood followed sagebrush by about 7 and 16 days respectively. Reduced vigor appeared to correspond to degree and duration of high water levels.

Extensive dieback of leafy bladder saltbush (*Atriplex vesicaria*) (1,130,000 to 531,000 ha reduction) occurred on the Riverine Plain area of southeastern Australia during 1979-1983 (Clift and others 1987). Widespread dieback occurred 2 years after an exceptionally high precipitation season. Although determining the cause was not an objective of their study, evidence seemed to implicate a causal link between waterlogging, increased salinity, pathogens, and insects followed by drought toward the end of the dieback period.

Certainly there were sites and instances during the recent high precipitation period in the Great Basin where waterlogging persisted long enough to cause shrub death directly or secondarily through plant predisposition by creating an environment conducive to microbial pathogen activity. In Rush Valley and other valleys of western Utah, in the zone where Wyoming big sagebrush and shadscale intermingle, there were instances of severe shadscale dieoff with little or no effect on sagebrush. Given that shadscale is more tolerant of waterlogging and salinity (perhaps not well established) one could conclude that other causal factors such as host-specific insects, microbial pathogen activity, or differential virulence of these agents between hosts, explain the differential mortality of shadscale and sagebrush.

Insect Epidemics

To affect the cross section of shrub species in the proportions observed in the recent dieoff would require a large-scale, multispecies insect epidemic. The nature and stability of the insect environment (weather, host, food state, predators, parasites, diseases, genetic polymorphism, and many other factors) interacting in complexity determine the latent or epidemic state of eruptive insects as reviewed by Wallner (1987). Primary epidemiological factors, influencing a broad spectrum of insects (such as a period of unusually high precipitation and consequent luxuriant growth of host plants) would be required to concurrently initiate the epidemic state of such a multispecies epidemic. In arid zones, weather fluctuations (precipitation, temperatures) tend to be more extreme than in humid zones. Aberrations in insect populations commonly follow extreme events and eruptive insects are usually more affected than endemic or non-outbreak insects. Both the direct and indirect influences of plant stress or stimulation result in an asynchrony in insect-host relationships. Examples of such altered relationships include: 1) increased phenotypic homogeneity, thus food supply; 2) modified host nutritional quality such as increased amino acid levels; 3) overwintering mortality of insects and consequent population genetic shifts; and 4) insect antagonist (predators, parasites, pathogens) population shifts (Wallner 1987).

A basic phenomenon of insect, as well as microbial epidemiology, is the conducive role of host geographic range, site-habitat uniformity, and host genetic homogeneity (monocultures). Shadscale frequently occurs in vast genetically homogeneous, fairly even-aged populations on rather uniform soils and sites as a result of recent shadscale evolution and occupancy of Pleistocene lake bottoms of the Great Basin by that species (Stutz 1978; Stutz and Sanderson 1983).

In their review of rangeland entomology, Watts and others (1982) noted the absence of information on browse plant insects of western North American rangelands, attributing the lack of detailed biological information to the ill-defined value of the resource to the ranching economy. Literature and observations on the impact of harmful insects and diseases on shrubs of western big game ranges (Furniss and Krebill 1972), and literature and unpublished data for insects affecting shrubs of the Pacific Northwest (Furniss and Barr 1975) have been reviewed and these publications again demonstrate a general lack of information in this area. The shrub species of interest in the foregoing reports are from the mountain-shrub zones associated with forest trees and riparian sites. An illustrative account of both beneficial and injurious rangeland insects of the western United States was published by the Four Corners Commission (1982). Haws and others (1988) prepared an index to information on insects of wildland shrubs of the western United States. Little experimental research has been conducted on insects associated with shrubs of the shadscale zone. There are, however, probably many rather obscure studies, primarily made by insect

collectors, that have indirect relevance to shadscale zone insect epidemiology. For example, lizards of the shadscale zone consume large quantities of a broad spectrum of insects (Knowlton 1934; Knowlton and Janes 1932, 1934). Thus, how do weather extremes or range management practices influence lizard populations?

Grasshoppers are of major importance on western rangelands, clearly surpassing all other insects in destructiveness (Anderson 1972). There are 13 grasshopper species in the intermountain region of potential threat (Hewitt 1977). Food habitat and host specificity vary among the species (Parker 1985; Sheldon and Rogers 1978) and, though not clearly understood, outbreaks appear to be closely related to the previous year's precipitation and additive daily temperature maximum thresholds (Gage and Mukerji 1977; Nerney and Hamilton 1969). Overwintering success, current hatch survival, and favorable weather for forage production are also involved. A large scale grasshopper epidemic occurred in central to northern Utah in 1984-1985, during the recent shrub dieoff period. Defoliation and debarking activity occurred on Utah juniper (Juniperus osteosperma), rubber rabbitbrush, big sagebrush, fourwing saltbush, shadscale, winterfat, and budsage (McCawley 1985). Based on a transect survey, various degrees of shadscale and black sagebrush mortality followed the severe defoliation of the previous year. The boundaries of shadscale dieoff, however, either did not correspond to the limits, or far exceeded the boundary of readily evident signs of grasshopper damage. Grasshopper feeding, thus, probably indirectly enhanced dieoff in some areas rather than being a direct cause.

The moth Aroga websteri is an important defoliator of sagebrush, especially species of the subgenus Tridentatae, throughout the Great Basin. Hsiao (1986) and Hsiao and others (1972-1976) have recently studied and reviewed the biology and demography of Aroga on big sagebrush. Substantial areas of sagebrush have been killed following several successive years of defoliation by Aroga. During the recent shrub dieoff, this defoliator apparently remained in a latent state and was not involved.

Another severe defoliator of sagebrush is the beetle, Trirhabda pilosa, reported to cause extensive damage in British Columbia (Banham 1961; Pringle 1960). There has been a recent report of isolated activity of Trirhabda sp. beetles on sagebrush in Utah (Haws and Boyer 1986), but no evidence of widespread activity of this insect in the Great Basin. Fourwing saltbush has been defoliated, and apparently killed, in southern Idaho by a beetle (Monoxia sp., Cyrtosomelidae) and casebearing moth larvae (Psychidae) (Meadows and others 1984).

A snout moth (Pyradidae) is reported to have damaged shadscale heavily on about 20,000 acres in the Raft River Valley of southern Idaho in 1951 (Hutchings 1952). Apparently because of associated mortality, the severe defoliation by the larvae was considered to be the cause of

death. No recent epidemic activity of this insect is known.

Similarly, Sharp and Sanders (1978) concluded that an infestation of shadscale between 1955-1958, also in southern Idaho, by a scale insect (Orthezia annae), (actually a mealybug-like insect, Homoptera:Ortheziidae) caused large-scale death of the host. Mealybugs have been observed on the upper taproots and lower branches of shadscale throughout the area of recent shrub dieoff in the Great Basin and adjacent areas. Scale insects and mealybugs have sucking mouth parts and damage plants directly by feeding or by injecting toxins. They can also transmit viral plant pathogens. Because of their feeding habit, evaluation of damage caused by these insects is more ambiguous than, for example, that caused by a defoliating insect. There is no experimental evidence available to demonstrate that mealybugs can kill shadscale; but based on agricultural crop experience (Rohrbach and others 1988), there is little reason to believe that a mealybug-virus complex cannot kill shadscale.

Plant Disease

Nature and Predisposition--Plant disease is an injurious physiological process induced by pathogenic agent(s). Plant pathogenic agents may be either biotic (fungi, bacteria, viruses, mycoplasmas, and others) or abiotic (temperature extremes, atmospheric toxicants, oxygen deficiency, mineral nutrient deficiency, and others). Vigorous, healthy plant growth increases host resistance to facultative parasites but is more favorable to infection and activity by obligate parasites. Physical (nongenetic) and biological environmental factors that are injurious initiate plant stress, thereby increasing susceptibility to potential pathogens (the plant is predisposed to disease development). In the absence of biotic pathogens and the cessation of nongenetic stress, the plant will recover. Nonaggressive facultative parasites commonly enter and become established in resistant as well as nonresistant plants, then remain latent until the plant becomes predisposed. Should predisposition occur, the disease process continues to develop and symptom expression takes place. Stress is thus more important in disease development than in parasitic establishment. A pathogenic mode of action common among facultative parasites is to kill host tissue in advance of the invading thallus and then to live saprophytically on the dead tissue, thereby determining the character of disease symptoms (such as tissue maceration or rot). The induction of increased host susceptibility by predisposing factors occurs through a variety of mechanisms: for example, the suppression of host defense-response systems.

The symptoms of shrub dieoff discussed above, if in fact induced by plant disease, are more typical of facultative parasites (wilt, root rot, rootlet necrosis) than obligate parasites (rust, smut, mildew). If plant disease is a major determinant in shrub dieoff, careful consideration of known predisposing factors and the presence of

facultative parasites seems relevant. Also important is the occurrence of an environment favorable for activity of these parasites; for example, water molds require a film of water in the soil for zoospore mobility. Successful infection and development of a disease usually require a rather intricate interaction of the host and pathogen in a common environment. Disease epidemics occur when a particularly favorable triangle of these elements occurs; this would differ to some degree with each host-pathogen-environment combination. For a facultative parasite a favorable triangle for an epidemic might include the following: 1) a genetically homogeneous host population, 2) an aggressive facultative parasite at an adequate population density, and 3) environmental stress factors optimal for host predisposition, yet favorable for parasite activity including antagonist relations.

Basic nongenetic environmental factors that stress plants, predisposing them to disease development include: 1) soil water-oxygen (drought and waterlogging); 2) stressful temperature (cooking, chilling, or freezing); and 3) toxicants (soil-water ions, atmospheric). Such factors predispose plants to disease by modifying or disrupting physiological processes: 1) metabolic production of toxins that inhibit parasites; 2) anatomical changes that form mechanical barriers against parasites; and 3) maintenance of critical carbohydrate levels. Biological predisposing factors that can act directly or indirectly through similar mechanisms include: 1) defoliation; 2) wounding; 3) rootlet "nibbling" by fungi or nematodes; and 4) loss of root symbionts (nitrogen fixing or mycorrhizal organisms). The foregoing discussion follows reviews on plant predisposition to disease by Yarwood (1959), Colhoun (1973), and Schoeneweiss (1975).

Considering the unusually high precipitation of the period (1977-1986) there would seem to have been adequate predisposing environmental conditions for disease of epidemic proportions (see above discussion on salinity-anaerobiosis). Prolonged stress (in the absence of biotic pathogens) related to physical soil factors acting individually or in combination could also have induced abiotic disease.

Fungal Pathogens--There is little information in the literature on diseases caused by facultative-type parasites for wildland shrubs of the sagebrush-shadscale zone. A number of Artemisia species were affected by a wilt and root rot disease in an experimental planting at Ephraim, UT (Nelson and Krebill 1981). Although the plants were growing in a heavy clay soil, it was a big sagebrush site prior to present agricultural use. Common facultatively parasitic fungal genera (Fusarium, Sclerotinia, Rhizoctonia, Alternaria, and others) were associated with the disease that was probably predisposed by abiotic soil factors and biotic factors incident to agriculture. Similar fungi were also associated with a basal-decay disease

commonly affecting fourwing saltbush on several wildland sites in Utah (Nelson and Welch 1984). During the apparent drought-induced dieoff of shadscale in Nevada (1976-1977), Fusarium was isolated from the roots and basal stems of dying shadscale (Nelson 1977-1978). Preliminary isolation studies on the recent dieoff reveal that similar associated fungi (Fusarium, Cephalosporium, Alternaria, Pythium) are present, not only in dying shadscale but also on associated low-vigor budsage and winterfat. These organisms can also be isolated from apparently healthy (symptomless) plants suggesting a pattern of infection, establishment, and subsequent latency. These fungal genera are cosmopolitan and include saprophytes as well as facultative parasites of a potentially pathogenic nature. They are apparently widespread components of the sagebrush-shadscale zone flora.

The rather insidious nature of damage to mature plants (reduced growth and vigor) caused by "root nibblers" such as Pythium has long been recognized (see review in Wilhelm 1965). Activity by this fungus could be an important biological predisposer to more virulent root rot or vascular wilt pathogens, especially during cool, high-precipitation periods that are favorable to its (Pythium) proliferation.

Among agricultural crops, members of the Chenopodiaceae, particularly Beta vulgaris, are vulnerable to this class of pathogens (Whitney and Duffus 1986) as well as others. A large group of these fungi (Pythium, Phytophthora, Phoma, Rhizoctonia, Fusarium, Verticillium) induces various diseases including: seedling damping off, root rot, leaf spot and blight, yellows, and vascular wilt.

Mycorrhizal Relations--Various reviews of research (Gerdemann 1968; Marx 1972; Marks and Kozlowski 1973; Mosse 1973; Zak 1964) primarily with forest trees, indicate that endo- and ectomycorrhizal fungal symbionts benefit the host in various ways such as: 1) deterrence of root pathogens; 2) absorption of both inorganic and organic nutrients, 3) increase of resistance to drought and high temperature damage, and 4) production of growth-regulating hormones. The mycorrhizal relations of sagebrush-shadscale zone shrubs have been little studied, but most species are probably mycorrhizal (Allen 1983; Gerdemann 1968; Lindsey 1984). Soil environmental factors known to influence mycorrhizae (Mosse 1973; Slankis 1974) include: 1) soil nutrient status (organic and inorganic), 2) soil moisture and oxygen levels, 3) soil pH, 4) presence and abundance of plant root exudates and fungal growth hormones, 5) rhizosphere effect, and 6) soil temperature. Failure of mycorrhizal symbioses, because of the adverse status of these factors and the subsequential influence on the host, could lead to plant stress. Potential instances when the above factors could have either benefited or damaged mycorrhizal associations have been discussed above with regard to the recent shrub dieoff. Because both mycorrhizal fungi and mycorrhizae are highly aerobic, the most likely factor to have affected

shrub mycorrhizae would be prolonged high soil moisture and associated anaerobiosis. Alteration of root physiology as well as a direct effect on mycorrhizal fungi, by anaerobiosis, could interact to the detriment of mycorrhizae and thus increase root susceptibility to pathogens. As further reviewed by Slankis (1974), numerous nonmycorrhizal fungi and some bacteria of the rhizosphere stimulate mycorrhizal infection and growth by release of extracellular thiamin and auxins. Thus deterrence of rhizosphere aerobes by anaerobiosis would tend to inhibit mycorrhizae and indirectly predispose hosts to disease.

Nematode Relations--Feeding by nematodes cannot only induce plant disease, but also nematodes can interact with plant viruses and fungal pathogens to adversely influence mycorrhizae. In their reviews, Endo (1975) and Powell (1971) described several nematode-fungus disease complexes (Fusarium and Verticillium wilt, Phytophthora root rot) and also described the role of nematodes in transmission of plant pathogenic viruses. Nematode feeding on ectomycorrhizal roots disrupts the fungal mantle and nutrient flow (Barham and others 1974). This not only damages the symbiotic association but also exposes rootlets to entry by other pathogens. Severe parasitic nematode damage to members of the Chenopodiaceae, particularly B. vulgaris, has been studied since the mid 1800's but the status of nematodes on chenopods of the shadscale zone remains unknown. Plant/parasitic nematode population dynamics are influenced by soil type, temperature, moisture, aeration, osmotic potential, organic matter, pH (Norton 1979), as well as biological interactions. Abiotic environments favorable to host vigor are also generally favorable to nematode activity (analogous to obligate fungal parasites). However, when plant stress factors subsequently occur that lower tolerance to nematodes, damage becomes more severe (Barker and Olthof 1976). Nematode damage generally tends to be less severe in heavy-textured soil than in light. The areas of more severe recent shadscale dieoff were where the soil was heavy. Thus there does not appear to be evidence for an environment particularly conducive to a nematode-caused epidemic in the recent shadscale dieoff.

Atriplex Genetics, Evolution, and Distribution

Plant populations confront the environment with an evolved "genetic system" ("the totality of the hereditary mechanisms controlling variability," Solbrig 1970). Character and amplitude of the system determine survival, continued evolution, or extinction of species in the face of stable to changing environments. Homogeneity of host genetics, host phenology, and host environment are among the critical elements conducive to insect and disease epidemics. Considering the nature of the various possible causal agents of the recent dieoff, discussed above, the status of soil environment is especially suspect (consider for example, soilborne biotic pathogens inducing root rot and vascular wilt; mealybugs that operate below the duff or soil surface).

Present populations of perennial Atriplex in and immediately around the Great Basin are thought to have migrated and evolved from populations of northern Mexico where adaptation through evolution in a desert environment has long existed. This might have occurred during a period of climatic aridity in western North America just prior to the last Bonneville pluvial about 12,000 years ago (Stutz 1978). Atriplex has apparently evolved a flexible system for synthesis of richly diversified genotypes through mutation, interspecific hybridization, allo- and autopolyploidy, and subsequent introgression and segregation (Stutz 1978). And as further portrayed by Stutz (1978), with the recession of Pleistocene lakes in what is now the Great Basin, new habitats were exposed in which a diversity of Atriplex genotypes were tested. The stage was thus set for an explosive evolution of new species.

Diploid Atriplex confertifolia (shadscale) populations apparently emigrated from areas peripheral to montane glaciers to occupy and evolve adaptation to upper elevation zones not submerged by developing Pleistocene lakes. Descendant diploid populations still remain in what is now the upper big sagebrush and pinyon-juniper zone (Stutz and Sanderson 1983). As the lakes receded and exposed topographically and edaphically new uniform habitats, shadscale populations began to be tested. Genetic combinations that by chance were uniquely suited to the new sites rapidly expanded horizontally across old lake bottoms to form sometimes vast almost pure stands of genetically homogeneous races (Stutz and Sanderson 1983). Barriers to outcrossing with bordering diploid populations tend to maintain the homogeneous integrity of new polyploid races. Chromosome analysis confirms the presence of diploid populations above the level of Pleistocene Lake Bonneville and races at various different polyploid levels below that elevation (Stutz and Sanderson 1983).

Contrary to the model of epidemiology in a dynamically balanced inter- or intraspecifically diverse natural plant community (Dinoor and Eshed 1984), that operating on the playas of Pleistocene lake bottoms in the Great Basin may be more analogous to that of an agricultural monoculture. Major portions of the shadscale zone could be climatically, edaphically, and plant genotypically homogeneous, and thereby a haven for pest outbreaks and dieoffs.

Considering the capacity for generation of genetic variability in Atriplex, should not evolution produce increasing resistance to factors that cause mass dieoff among taxa of the genus? Or, as a contrary, speculation could suggest that vulnerability to mass dieoff is a mechanism for plant redistribution on the site, from islands of shadscale halophytic salt accumulation. Demographic factors such as mechanisms for preservation of seed stores to survive "needed" dieoffs could be more important than dieoffs to the long-term survival of shadscale. Perhaps the more basic problem is to reconcile range management interests with a largely unknown

shadscale ecology, while protecting its "genetic-system" store from a too-abrupt man-caused environmental change, such as the introduction of weedy exotic and perceived desirable plants into the shadscale zone.

SUMMARY-CONCLUSIONS

Overuse of shrubs by ruminant animals can be largely discounted as a cause of the recent dieoff. Overgrazing could possibly function as a secondary weakening factor and then only in restricted areas as in the case of fourwing saltbush stands in Dry Valley, San Juan County, UT, and in Wyoming big sagebrush stands on Taylor Flat, Browns Park Area, Daggett County, UT. In the majority of dieoff areas, there is seldom evidence of overgrazing.

Symptoms and patterns of the dieoff events of 1984-1985 discount winter injury as a cause, except in a few cases. Death of bitterbrush and big sagebrush occurred in an elevational belt among the east side of Skull Valley, Tooele County, UT (spring of 1985). That episode was suggestive of winter injury during a valley temperature inversion, because the damaged area followed a sharp line across a uniform population of mountain big sagebrush above which no injury occurred.

Although there is some good evidence to establish drought and associated factors as the major cause of episodic shadscale dieoffs prior to 1977, the recent dieoff was associated with an historically high precipitation period, not drought.

Salinity and anaerobiosis are soil environmental factors likely to be associated with extended high precipitation periods. In areas subject to high water tables or in small depressions and large basins where impervious soil strata would impede soil-water drainage, prolonged waterlogging and thus anaerobiosis is likely to occur. Considering the geomorphology of the Great Basin and adjacent areas, these sites must be common. Both excessive salinity and prolonged anaerobiosis can kill plants directly, induce abiotic disease, or predispose plants to biotic pathogens. However, there are many extensive and small or scattered dieoff sites in the shadscale zone (mid-valley rises, slopes, and ridges) where prolonged waterlogging, even during high precipitation, is unlikely.

Insects in a latent or endemic equilibrium state do some damage to plants without resulting in mass dieoff. The majority of insect species associated with dieoff in the shadscale zone were undoubtedly in an endemic (nonoutbreak) state. Most species, such as the Aroga sagebrush defoliator, known to cause large-scale death when in an epidemic state, were not obvious during the recent dieoff. The grasshopper epidemic occurring in 1985 caused severe damage but was far more limited in scope than the dieoff phenomenon. The mealybugs of shadscale could cause major dieoffs based on agricultural parallels, but this does not account for dieoffs

in all areas or of other shrub species. The single report of shadscale damage from mealybugs does not associate the epidemic with high or low precipitation.

Soilborne microorganisms, soil salinity, and anaerobiosis seem to be the environmental factors, of those considered, that would be modified or enhanced the most by high soil moisture extremes. Prolonged springtime high soil moisture could favor the proliferation of facultative soilborne parasites such as Pythium. Pythium-induced fine feeder-rootlet mortality could result in plant predisposition to other pathogens (Fusarium) or result in desiccation and nutrient stress during low-moisture periods of summer. These fungi generally have wide distribution and a wide range of hosts. Dieoff could then be possible on sites having extended high soil moisture but insufficient for high salinity and prolonged anaerobiosis. Plant stress, from all other factors considered in this discussion, could influence plant predisposition to disease development. The range in severity of dieoffs could result from variable interaction of these factors and the subsequent degree of predisposition.

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ARE WILDLAND PLANT COMMUNITIES A POTENTIAL SOURCE OF UNDERSTANDING
BIOLOGICAL RESPONSES TO IRON-DEFICIENCY STRESS?

Sheldon D. Nelson and Von D. Jolley

ABSTRACT: Iron deficiency is a serious problem for many cultivated crops in arid regions with predominately calcareous soils, but is rarely observed in wildland shrub-grass ecosystems. The economic importance of iron deficiency in cultivated species has motivated investigations concerning plant response to iron stress and has provided evidence for several proposed mechanisms including: (a) various combinations of increased root excretion of hydrogen ions and reductants, higher levels of chemical reduction enzymatic activities, and organic acids within the root, and changes in root morphology in Fe-stressed dicotyledenous plants; (b) release of phytosiderophores (iron chelators) by the roots of Fe-stressed graminaceous plants. The former mechanism, currently designated Strategy I, supposes a solubilization of soil iron and reduction processes to make iron available to plants. The latter mechanism, designated Strategy II, supposes an extrusion of phytosiderophores with highly selective affinities for iron to enhance uptake. In addition, hydroxamate siderophores produced by fungi and bacteria during iron-stress conditions may provide an important iron supply to roots of both plant types. The understanding of these mechanisms has been developed almost exclusively from the study of domesticated species. It has been postulated that plants could not obtain iron in arid land soils without these factors modifying iron solubility. However, virtually nothing is currently known about the factors which allow wildland species to thrive in arid soils.

INTRODUCTION

Wildland plants of arid regions have adapted to harsh biological environments in which extremes and fluctuations in temperature, moisture, salinity, radiation and nutrients are common and in which growth limiting factors due to soil physical and chemical properties are normal. Some plants thrive in soils that are droughty, calcareous, high in pH, low in organic matter and iron solubility. However, in the case of iron, little is known about the successful adaptation of a wide variety of organisms under these harsh conditions.

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Iron is an essential element for plants which is most efficiently supplied through vigorous new root growth in diffusion-controlled processes. Iron availability is enhanced by low pH, adequate moisture and balanced nutrition (O'Connor and others 1971; Chaney 1984). Well-aerated alkaline soils predictably contain inadequate quantities of available iron for higher plants because high pH and unsuitable redox potentials diminish iron solubility (Lindsay 1979). Soluble inorganic iron levels in calcareous soils of at least two orders of magnitude less than the potential requirement for plants (Schwab 1981) are evidenced by iron chlorosis of many introduced cultivated crops (Nelson and others 1982). Some introduced species do not survive the induced iron stress because they lack adaptive mechanisms, whereas wildland plants seldom exhibit iron-stress chlorosis due to insufficient iron uptake. In adapted (Fe-efficient) cultivated species, iron mobilization and uptake occurs in the apical region of roots (Brown and Ambler 1973), where root-induced solubilizing and chelating processes chemically alter the rhizosphere environment. These iron-stress response mechanisms have recently been reviewed (Romheld and Marschner 1986; Wallace 1987; Brown and Jolley 1988). Although native plants have apparently developed mechanisms to allow iron uptake in a hostile environment (Brown 1977; Nelson and others 1982), virtually no understanding of the mechanisms in the native plants has been accumulated. The purpose of this paper is to review the current knowledge of iron-stress response in cultivated species and to suggest that the study of native wildland plants may hold a potential for further understanding of biological responses to iron stress.

DISCUSSION

Classification of Plant Response Mechanisms

Crop species or cultivars which grow in conditions with high potential for development of iron chlorosis (i.e. calcareous, high pH, high phosphorus, cation imbalance, or low iron) without becoming chlorotic have been classified as iron efficient. Those which do develop chlorosis under these conditions are referred to as iron inefficient. The iron-efficient cultivars have developed specific mechanisms which mobilize iron and allow its uptake, while the iron-inefficient cultivars do not. However, mobilization of iron can also be stimulated by nonspecific mechanisms. The latter mechanisms are not related to the iron nutritional status

nor to the Fe-efficient or Fe-inefficient nature of the plant, but to normal plant processes. Both types of mechanisms will be discussed briefly in this review.

Nonspecific Iron-Uptake Mechanisms

Plant roots excrete hydrogen ions into the bulk solution due to preferential cation uptake. This release increases iron solubility, lowers redox potential, and consequently makes iron reduction and subsequent uptake possible (Wallace and others 1968; Brown 1977; Lindsay 1979, 1984; Bienfait and others 1982a; Fleming and Foy 1982; Johnson 1982; Varanini and Maggioni 1982; Hershey and Paul 1984). The amount of hydrogen ion release is dependent on excess base/nitrogen ratio (ratio of cation to anion uptake), the form of nitrogen (ammonium or nitrate) absorbed, and the phosphorus nutritional status of the plant (Marschner and Romheld 1983; Romheld and Marschner 1986).

Organic acid extrusion into bulk soil solution by roots can potentially increase iron solubility through acidification as well as through reduction and chelation (Gardner and others 1983; Young and Terry 1984; Romheld and others 1984).

Sloughed cells and root exudates increase microbial activity in the rhizosphere, which can cause lower redox potential, acidification and improved iron uptake. Phytosiderophores exuded by higher plants become iron chelators and will be discussed under specific iron-stress response mechanisms.

Microbial production and release of chelating compounds and siderophores may have a significant impact on the iron nutrition of higher plants (Trolldenier 1973; Barber and Lee 1974; Emery 1977, 1982; Sauerbeck and others 1982; Powell and others 1982; Rodriguez and others 1984). This chelation process can increase the solubility and availability of iron to roots of higher plants (Orlando and Nielands 1982; Cline and others 1984) through the increased concentration of siderophores within the root zone (Reid and others 1984). Beneficial effects of microbial siderophore release have been demonstrated in sunflower, peanut, tomato, duckweed, sorghum and oat, but the extent and importance of this natural chelation process has yet to be quantified in the ecology of wildland plants.

Specific Iron-Stress Response Mechanisms

Strategies for Iron Uptake--Recently, two broad strategies of plant response to iron deficiency stress have been proposed (Romheld and Marschner 1986). Plants with the more complicated Strategy I mechanisms are dicots and nongramineous monocots. The iron-stress responses characteristic of Strategy I plants include: formation of rhizodermal transfer cells or increased formation of root hairs, enhanced release of hydrogen ions, release of phenolics or "reductants", increased levels of citrate in roots, and enhanced iron (III) reduction at the plasma

membrane (Brown and Ambler 1973, 1974; Landsberg 1982). However, not all Fe-efficient species exhibit the full complement of responses. Only grasses have been found to exhibit the Strategy II mechanisms in which root release of phytosiderophores results in chelation of inorganic iron (III) and subsequent transport to and absorption through the plasma membrane by a highly specific uptake system and in the absence of any iron reduction processes.

Of the two proposed strategies for responding to Fe stress, Strategy I has been most extensively studied. Because the Strategy II mechanisms have only recently been discovered, they have been less extensively studied and may seem more simplistic. In addition, Brown and Jolley (1988) suggest that it may be too early to finalize the division of plants into two simple categories. A more extensive description of the mechanisms of both Strategies follows.

Hydrogen Ion Extrusion from Modified Root Systems--Enhanced production of protons is nearly universally present in plants exhibiting the Strategy I response. This acidification is specifically invoked under Fe-deficiency stress conditions and is reportedly associated with a plasma membrane ATPase driven proton pump (Landsberg 1982). It is often associated with morphological changes of roots such as diminution of apical roots, abundant root hairs or formation of rhizodermal transfer cells. These specialized root characteristics are also the site of active iron uptake during iron stress (Wallace and others 1968; Landsberg 1982, 1984; Romheld and others 1982; Romheld and Kramer 1983).

Excretion of Reductants--Iron (III) is reduced to the more plant available form [iron (II)] when specialized "reductants" are released by plant roots during iron stress (Brown 1961, 1977; Brown and Ambler 1973; Olsen and others 1982; Wallace 1983; Hether and others 1984; Kannan and others 1984). These reductants are effective in reducing iron at low pH (4.5) and are closely associated with the other Fe-deficiency-induced changes in the roots of dicots (Camp and others 1987).

Enzymatic Iron Reduction--Iron (III) is reduced enzymatically at the outer surface of the plasmalemma of roots (Chaney and others 1972; Beinfait and others 1982a, 1982b, 1984; Barrett-Lennard and others 1983; Tipton and Thowsen 1983; Campbell and Redinaugh 1984; Sijmons and Bienfait 1984; Uren 1984; Wallace and others 1984; Camp and others 1987). This reduction is important as iron (II) is the predominate form absorbed by dicotyledenous species. This reduction is also closely linked to other parts of the Fe-stress response mechanism (Camp and others 1987).

Accumulation of Citrate in Roots--Before iron reduced at the plasmalemma is transported to the

plant tops it is oxidized [iron (III)] and complexed with citrate in the xylem. Several investigators have reported a build up of citrate and other organic acids in iron-stressed plants, and Fe-efficient cultivars contain higher levels of root citrate than Fe-inefficient cultivars (Clark and others 1973; Brown 1977).

Release of Phytosiderophores--Under conditions of iron-deficiency stress, oat, barley, and rice released iron-chelating compounds similar to those produced by microorganisms. Chelation of iron and subsequent uptake through root production of phytosiderophores is particularly active in species belonging to Gramineae, but has not been identified in dicots (Peters and Warren 1970; Takagi 1976; Nielandt 1977; Raymond 1977; Takemoto and others 1978; Nomoto and others 1981; Fushiya and others 1982; Mino and others 1983; Reid and others 1984; Rodriguez and others 1984; Takagi and others 1984). Phytosiderophores of barley and oats have been characterized as the nonproteinogenic amino acids, mugineic acid and avenic acid, respectively (Fushiya and others 1982). Following the iron-stress response of increased release of phytosiderophores, production of phytosiderophores declines within 24 to 48 hours when sufficient iron is supplied (Takagi and others 1984).

Uptake of iron by monocots under iron stress is presumed to be as iron (III). However, Crowley and others (1988) suggest that there are siderophore binding sites on the plasmalemma of oat root cortical cells wherein iron uptake occurs by extraction from the organic chelating molecule through enzymatic reduction of iron (III) to iron (II).

The pH (pH 4-8) does not substantially affect the production nor activity of phytosiderophores, whereas the release of reductant in non-gramineous plants is highly pH dependent and iron reduction through this process occurs much slower than phytosiderophore chelation (Takagi 1976; Romheld and Marschner 1983). Phytosiderophores are not always iron specific and chelation with copper and zinc and other elements is not uncommon, thereby influencing the release of additional essential micronutrients (Takagi 1976; Benes and others 1983).

CHALLENGE

Iron uptake mechanisms of cultivated species have been extensively studied and significant progress has been made to understand the processes involved. At best, two strategies have been identified in these crops, but an understanding of the mechanisms involved is far from complete. Wildland species seldom exhibit iron deficiency chlorosis, however one assumes that they are exposed to an adverse iron-uptake environment. To date, there is no existing evidence that the mechanisms known to function in cultivated crops even exist in wildland species. Identification and investigation of the mechanisms involved in wildland species seems critical to a complete

understanding of iron nutrition in plants. Wildland species may be a valuable key in the development of new iron efficient crops and ornamental species for the vast areas of calcareous soils throughout the world.

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EFFECTS OF HEAVY GRAZING BY MULE DEER ON 'HOBBLE CREEK' MOUNTAIN BIG SAGEBRUSH SEED STALK PRODUCTION //

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ABSTRACT: On 'Hobble Creek' mountain big sagebrush (Artemisia tridentata ssp. vaseyana) native range there is a recruitment problem. One factor contributing to this problem could be a dramatic reduction in seed production due to continuous heavy grazing (utilization of 70 percent or more of current year's growth) by wintering mule deer (Odocoileus hemionus hemionus). A deer-proof enclosure was constructed on the native site to test the effects of heavy grazing on productivity as measured by length of current year's growth, length of seed stalks, and number of seed stalks per plant. Productivity was not significantly different between grazed and nongrazed plants (13.9±2.2 vs 12.9±2.1 cm). Seed stalks of nongrazed plants were significantly longer than those of grazed plants (26.6±1.2 vs 15.8±3.5 cm). Nongrazed 'Hobble Creek' plants produced not only significantly longer seed stalks but greater numbers of seed stalks per plant than grazed plants (172.4 vs 6.1 seed stalks). A dramatic reduction of seed numbers could be one factor responsible for lack of recruitment on the native site.

INTRODUCTION

'Hobble Creek' mountain big sagebrush (Artemisia tridentata ssp. vaseyana) is a superior selection that can increase the nutritive content of the winter diet of mule deer (Odocoileus hemionus hemionus) and domestic sheep (Ovis aries) (Welch and McArthur 1979; Welch and others 1987). This selection of big sagebrush has higher amounts of winter crude protein, phosphorus, carotene, and higher in vitro digestibility than other species of shrubs, grasses, or forbs (Bunderson and others 1986; Welch and others 1986). As a big sagebrush it is slightly below average for these nutrients but is preferred over other selections by wintering mule deer and ranks among the most preferred by wintering domestic sheep. 'Hobble Creek' was released (1987), as the first superior selection of big sagebrush, as a forage plant on mule deer and domestic sheep winter ranges (Welch and others 1986).

A problem observed on 'Hobble Creek' native range is the lack of seedlings or young plants

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(5 years old or less). We believe this lack of recruitment is due to one or more factors: 1) killing of seedlings and young plants due to heavy grazing, 2) grass understory competition not allowing seedling establishment, and 3) reduced seed production due to heavy grazing. Heavy grazing is defined as utilization of 70 percent or more of current year's growth. The last factor, reduction of seed production, is the subject of this study. Factors 1 and 2 are being studied by other researchers.

Reduced seed production means fewer opportunities for seedling establishment. An indicator of reduced seed production would be reduction in the numbers and length of seed stalks produced per plant. A single big sagebrush seed stalk can produce several thousand seeds (McArthur and others 1979; Welch and McArthur 1979). The hypothesis tested was that nongrazed 'Hobble Creek' big sagebrush plants produce greater numbers of seed stalks and longer seed stalks than heavily grazed plants. We also tested the hypothesis that nongrazed plant productivity measured in terms of length of current year's growth would be greater than heavily grazed plants.

MATERIALS AND METHODS

On the 'Hobble Creek' big sagebrush native range, a deer-proof enclosure 100 by 50 by 8 ft (30.48 by 15.24 by 2.44 m) was constructed to provide nongrazed plants. The location of the enclosure is about 2 miles (3.2 km) east of Springville, UT, at the mouth of Hobble Creek Canyon (section 36, R3E, T7S). Plants outside the enclosure receive use on better than 70 percent of current year's growth by wintering mule deer.

A 200-ft (60.96 m) line transect was established through the middle of the enclosure. The line extended 50 ft (15.24 m) beyond either side of the 100-ft enclosure. Along this transect, 10 nongrazed and 10 grazed plants were selected for measurements. The 20 plants were chosen by starting at the east point of the transect and tagging with a metal numbered tag every third plant until 10 grazed and 10 nongrazed plants had been tagged.

Plant measurements were taken during mid-November of 1984 and 1985 and were expressed as length of vegetational current year's growth, length of seed stalks, and number of seed stalks per plant. Length of vegetative current year's growth was determined by measuring 15 leaders per plant. Randomly selected leaders were

measured from the terminal leaf bud scars to the tip of the terminal leaves. The 15 measurements were pooled together for a plant mean. Length of seed stalk was determined by measuring 15 or, in the case of most grazed plants all, seed stalks. The seed stalks were measured from the terminal leaf bud scars to the tip of the seed stalk. Where possible, seed stalks were selected at random over the entire crown of the plants. All measurements per plant were pooled together for a plant mean. Measurements were taken during mid-November of 1984. The third measurement, number of seed stalks, was a simple counting procedure. Seed stalk counting was done during mid-November of 1984 and 1985.

Statistical analysis performed was a one-way analysis of variance to detect differences between grazed and nongrazed plants (in some cases used to detect differences between year for grazed or nongrazed plants). We used the Minitab Statistical package (Ryan and others 1976) and significance was set at $P=0.05$.

RESULTS AND DISCUSSION

Results of the length of current year's growth analysis are given in table 1. Due to the lack of significant effects due to years the 2 years of data were pooled. Nongrazed plants (13.9 cm) were not significantly longer than grazed plants (12.9 cm). This observation is in agreement with a study conducted by Wright (1970). Wright found that an 80-percent clipping treatment during the winter months of December and January did not significantly reduce yields. However, Cook and Stoddart (1960) reported that a 50-percent clipping treatment applied about March 1 reduced plant vigor. Garrison (1953) reported that a 10 percent clipping treatment during winter actually

Table 1--Comparison between mean length of current year's growth of grazed and ungrazed 'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). Means are a 2-year average. Data expressed as centimeters of growth

Plant #	Grazed (cm)	Nongrazed (cm)
1	12.9	14.2
2	12.1	15.7
3	14.3	12.5
4	10.5	13.1
5	11.7	15.5
6	14.7	13.5
7	12.4	13.1
8	12.7	13.3
9	13.2	12.9
10	14.4	15.2
Mean	¹ 12.9±2.1	¹ 13.9±2.2

¹Means are not significantly different at the 5-percent level.

increased the length of current year's growth for antelope bitterbrush (*Purshia tridentata*), snowbrush ceanothus (*Ceanothus velutinus*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and creambush rock spirea (*Holodiscus discolor*). He went on to make two observations: first, that continued 100-percent clippings after about 5 years decreased plant vigor and, second; seed production was greatly reduced in direct response to clippings. Based on our observations, and those cited, heavy grazing on 'Hobble Creek' big sagebrush does not reduce the length of current year's growth but over a period of time could cause reduced vigor and increased branch mortality resulting, in time, in entire plant death.

Comparisons of the length of seed stalks are given in table 2. Nongrazed plant seed stalks were significantly longer than those of grazed plants (15.8 vs 26.6 cm). This suggests that nongrazed plants with equal numbers of seed stalks would probably produce more seeds because of greater length of seed stalks.

Table 2--Mean lengths of seed stalks of grazed and ungrazed 'Hobble Creek' mountain big sagebrush plants (*Artemisia tridentata* ssp. *vaseyana*). Data are expressed as a mean of 15 measurements per plant. Measurements are given in centimeters

Plant #	Grazed	Nongrazed
1	12.0	25.4
2	14.7	25.5
3	0	25.2
4	22.5	27.2
5	18.5	26.6
6	22.0	26.5
7	23.0	26.5
8	24.5	28.1
9	20.4	26.8
10	0	28.3
Mean	¹ 15.8 ±3.5	¹ 26.6 ±1.2

¹Means of 1984 and 1985 growth. Means are significantly different at the 5-percent level.

The number of seed stalks are compared in table 3. Because of significant differences between years for nongrazed plants, years were not pooled. Nongrazed plants produced significantly more seed stalks (116.8-1984, 228.0-1985) than grazed plants (6.1-1984, 6.2-1985). These observations do not agree with the findings of Cook and Stoddart (1960). They reported significant reduction in number of seed stalks for 50-percent clipped plants in only 1 year of a 3-year study. Their magnitude of difference in the significant year was 32.5 seed stalks while our magnitude was 110.8 for 1984 and 222.6 for 1985. Unfortunately, we do not know what subspecies Cook and Stoddart (1960) were studying or the grazing history of the plant. Our plants had been heavily grazed (70 percent or more) for at least 5 years prior to beginning this study.

Table 3--Comparison between number of seed stalks of 1984 and 1985 grazed and 1984 and 1985 nongrazed 'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) plants

Plant #	1984 Grazed # of seed stalks	1984 Nongrazed # of seed stalks
1	1	182
2	6	33
3	0	122
4	10	77
5	6	61
6	8	157
7	2	172
8	2	81
9	26	126
10	0	157
Mean	¹ 6.1±7.8	¹ 116.8±51.3
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	1985 Grazed	1985 Nongrazed
1	1	389
2	7	108
3	8	207
4	10	256
5	55	189
6	10	210
7	2	226
8	0	236
9	18	198
10	1	261
Mean	¹ 6.2±5.6	¹ 228.0±71.0
Two-year means	6.1±6.6	172.4±83.0

¹Means are significantly different at the 5-percent level. Two-year means not statistically tested due to significant year effects for nongrazed plants.

Under the conditions of our study, we believe that one factor that is contributing to the lack of recruitment on the 'Hobble Creek' big sagebrush native site is a dramatic reduction in seed numbers due to heavy grazing.

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INTERACTION OF STRESSES IN THE BEHAVIOR OF NATIVE SHRUB POPULATIONS //

Arthur Wallace

ABSTRACT: The vegetation of arid lands faces severe stresses of many kinds and under natural conditions. Even though shrubs are reasonably adapted to the stress conditions, they are affected by the stresses. Ordinarily, adapted plants can tolerate degrees of the stresses, but are limited with increasing levels of stresses. Of extreme importance for increasing multiple stresses is that there is much evidence that sequential additivity and even synergism operate for the multiple stresses. Natural stresses that are common to arid lands include heat, drought, wind, salinity, floods, infertile soil, and animal pressure. The addition of man-induced stresses can be devastating if sequential additivity is operating because the effects of stresses are then multiplied. Examples of multiple stresses are that shrubs may be more subject to ionizing radiation if they are simultaneously stressed with drought or with other natural stresses, or acid rain may be more damaging to a waterlogged area than to a nonwaterlogged area, or that toxic levels of more than one trace element simultaneously may be more damaging than one trace element in excess. Although many stresses can be sequentially additive, this is not always the case.

INTRODUCTION

It is well recognized that arid-land ecosystems are extremely fragile and that many uses of them by man lead to their deterioration (Anonymous 1980). Expanding deserts or desertification has been a serious worldwide problem, and in recent decades there have been attempts to control desertification (Anonymous 1980; Norman 1987). Efforts, however, have resulted in little success, and it is reported that "an overwhelming majority of anti-desertification projects would promote desertification" (Norman 1987).

Such problems are of considerable concern to those who manage wild shrub communities in arid lands. Disturbed communities recover very slowly. Those persons involved in land revegetation realize that

it is much more complex than merely planting seeds or placing transplants. Multi-components of the ecosystem may need to be restored, especially those related to symbiosis (Wallace and others 1980).

REASONS FOR FRAGILITY OF ARID LAND ECOSYSTEMS

In recent years it has been becoming apparent that one of the central principles of biology is the interacting nature of environmental forces, including the availability of resources that organisms require which originate in the environment. It is a general rule that the environmental factors can interact sequentially additively or positively or negatively synergistically (Berry and Wallace 1981; Putman and Penner 1974). Interactions like this are common in agriculture (Anonymous 1974; Fjell and other 1984; Wallace and others 1981a). Arid ecosystems naturally have several different harsh components, and survival of organisms in such areas requires special adaptations. Even with the adaptations, the situation is very borderline or fragile for plant survival under such conditions (Wallace 1987).

Arid ecosystems by definition are in areas having low amounts of rainfall. Low amounts of rainfall can differ with multiple possibilities. There can be varying degrees of infrequency. Seasonality makes large differences in the ability of the rain water to sustain a system. Volume and intensity of rain with associated runoff or run-in are important parameters. Runoff can be associated with soil erosion.

Arid-ecosystems in varying degrees are usually also associated with hot climate. Because of hot climate and low amounts of vegetation, soil is poorly developed, nutrient poor, and shallow. Because of low rainfall, arid soils are usually highly calcareous. Restricted soil-forming processes, enhanced by low rainfall and small amounts of vegetation, limit removal of calcium carbonate from soil. Because soils are poorly leached and subject more to chemical degradation than to biological degradation, large quantities of soluble salts, including sodium chloride, are often present.

Shallow soils almost devoid of soil organic matter are easily eroded by water and wind. An associated sparse vegetation can lead to a degree of stability. However, if destroyed or replaced by a different vegetation which may be subject to some of the stresses listed above, the shallow soil may erode away.

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MAN-MADE STRESSES IN ARID LAND ECOSYSTEMS

There are a number of man's operations that add stresses to arid-land ecosystems.

Overgrazing

This is perhaps the most common man-made stress that adds to the instability of arid lands. It has been a problem for many millenia. Overgrazed lands recover only very slowly.

Scraping or Bulldozing

Construction results in considerable destruction of native arid lands. Sometimes a bladed area is needed for temporary activities. Lands are then abandoned to erode or to remain unvegetated for a long period of time.

Water Diversion

Owens Valley in California is a well-known example of water diversion. The Los Angeles aquaduct carries water from the valley to the City of Los Angeles some 500 km away. In the past 80 years, the usual flow of water into the native shrub ecosystem has been decreased with the resulting added stress.

Agriculture

Shrub ecosystems in arid lands are constantly being replaced with irrigated agriculture. A scenario on how such land reclamation can increase the instability of arid lands has been presented (Wallace 1988).

Differential Shrub Removal

Herbicides and mechanical equipment have been used to differentially remove some shrub species from native ecosystems. The reason is to enhance growth of other plants in the ecosystems. This could relieve one kind of stress and cause others.

Off-Road Vehicle Use

Tire tracks and temporary roads in arid lands do result in erosion and other types of degradation.

Mining

Mining activities result in many different types of impacts on arid lands, including many of those listed above. Additional stresses may come from the chemical nature of material being mined, especially trace elements (Wallace and others 1981b).

SEQUENTIAL ADDITIVITY AND SYNERGISM

If stress "a" decreased biological activity by 20% and stress "b" decreased it by 40% when applied

separately, the combined biological activity for both together may be 48% or a 52% decrease. The result would be a sequentially additive interaction (Berry and Wallace 1981). Such interactions imply that $\frac{(100-20\%)}{100} \times \frac{(100-40\%)}{100} = \frac{48\%}{100}$. If the biolog-

ical activity for the combination were decreased by significantly more than 52%, the interaction is synergism (table 1). A decrease of significantly less than 52% would indicate a positive interaction (table 1). If, however, the combination of "a + b" increased rather than decreased the biological activity, the result is a negative synergism. Figure 1 further describes the nature of interactions. Only one level of stress "b" is used.

In table 1 it is shown that when the actual/predicted ratio is 1.00, an interaction is additive. Positive interactions would give values slightly below 1.00, and negative interactions would give values slightly above 1.00. Positive synergism would give values much less than 1.00, and negative synergism would give values well over 1.00. There could be complications if a and b have the same biological action.

The data of table 1 indicate the type of experiments needed to determine the type of interaction that may result from two or more stresses. Each pair or group of stresses must be handled separately for a given system, and the effect of each stress individually must be known in order to assess the nature of an interaction.

The most common type of interaction encountered for multiple stresses is the sequentially additive (Berry and Wallace 1981). These effects constitute a threat to the stability of arid ecosystems. For example, if five different stresses each decreased biological activity in an arid ecosystem by 50%, the combined effect could result in a final activity of only 3% if all interactions were sequentially additive. The activity could be even less if positive synergism came into play.

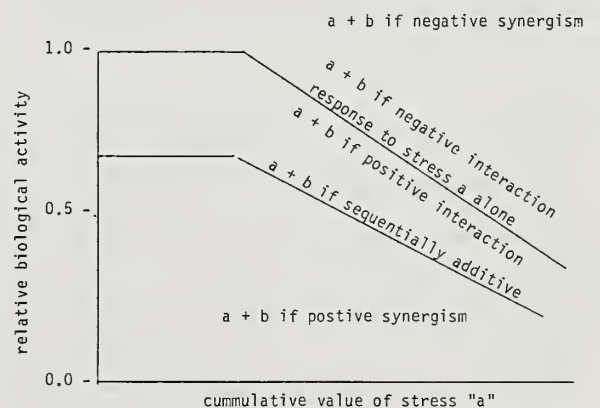


Figure 1--Possible interactions for two stresses ("a" and "b") acting simultaneously.

Table 1--Some possible responses on plants when two different stresses (a and b) interact simultaneously

Stresses	Relative growth or reproduction	Comments	Actual/predicted ratio
Situation 1--Response individually to only one of the stresses			
Control or no stress	1.00	--	--
a	1.00	no change	--
b	0.50	large decrease	--
a + b	0.50	expected if there are no interactions, the predicted or the additive value	1.00 or $0.50 \div 0.50^1$
a + b	1.25	negative synergism (antagonistic)	2.50 or $1.25 \div 0.50$
a + b	0.40	postive interaction	0.80 or $0.40 \div 0.50$
a + b	0.60	negative interaction	1.20 or $0.60 \div 0.50$
a + b	0.25	postive synergism	0.50 or $0.25 \div 0.50$
Situation 2--Responses individually to both the stresses			
Control or no stress	1.00	--	--
a	0.60	large decrease	--
b	0.60	large decrease	--
a + b	0.60	this would be the result if a and b each had the same effect and if 0.60 were the maximum response possible; neutral or no interaction	1.67 or $0.60 \div 0.36^1$
a + b	0.36	fully additive; the interaction predicted	1.00 or $0.36 \div 0.36$
a + b	0.55	negative interaction	1.53 or $0.55 \div 0.36$
a + b	0.30	positive interaction	0.83 or $0.30 \div 0.36$
a + b	0.15	positive synergism	0.42 or $0.15 \div 0.36$
a + b	0.80	negative synergism (antagonistic)	2.22 or $0.80 \div 0.36$

¹The 0.50 and 0.36 are the products of a x b each acting individually.

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SEED GERMINATION BIOLOGY OF ANTELOPE BITTERBRUSH (PURSHIA TRIDENTATA) //

Susan E. Meyer and Stephen B. Monsen

ABSTRACT: Dormancy-breaking experiments with seeds from 28 antelope bitterbrush populations revealed no clear relationships between the degree of dormancy of recently harvested seeds and habitat characteristics at the site of seed collection. Afterripening in dry storage shortened the chilling requirement for germination, while interruption of prechill with a warm, moist period lengthened the chilling requirement. Postdispersal conditions for this summer-ripening species may have an important effect on the degree of seed dormancy at the initiation of field chilling and thus on chilling requirements and subsequent germination date.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata) is widely distributed in the western United States and is an important component of the diet of mule deer and other native ungulates (Giunta and others 1978). Because of its importance in restoring depleted wildlife habitat through artificial seeding, antelope bitterbrush is one of the most intensively studied of all wildland shrubs (Basile 1967; Tiedemann and Johnson 1983). Its seed production and dispersal, germination, and seedling establishment ecology have been the subject of numerous studies (Evans and Young 1977; Ferguson 1962; Holmgren 1956; Hormay 1943; Shaw and Monsen 1983).

Antelope bitterbrush seed is dormant at the time of dispersal in early to midsummer and requires a period of moist chilling to germinate (Young and Evans 1976, 1981). Under field conditions, seeds apparently germinate in early spring, at a time when adequate soil moisture for successful establishment coincides with reduced risk of frost to the newly emerged seedlings (Ferguson 1972; Nord 1965).

Antelope bitterbrush seeds are quite large (mean weight of 100 seeds=2.95 g, n=28), and the chances for successful establishment of surface-lying seeds are poor. Moreover, the conditions necessary for breaking dormancy are not likely to persist for long enough on the surface, except

possibly under snowpack. Artificial seeding techniques that do not include provision for seed burial are rarely successful (Basile and Holmgren 1957). Under natural conditions, seeds are often cached by rodents, and emergence takes place from cached seeds (Evans and others 1983; Sanderson 1962; Sherman and Chilcote 1972; West 1968).

The timing of antelope bitterbrush seed development is affected by site conditions, with populations on hotter, drier sites maturing seed first. The seeds on an individual plant and even within a population tend to mature synchronously. When accessions from a range of habitats are grown in a common garden, between-accession differences in seed maturation dates are much less than would be encountered in the original wild populations (Shaw and Monsen 1983).

Antelope bitterbrush is important over a wide range of habitats, from sagebrush-grass steppe vegetation where annual precipitation is less than 200 mm to lodgepole and ponderosa pine forests where annual precipitation may exceed 800 mm (Nord 1965). The average length of time between seed dispersal and the initiation of a moist chill period varies according to habitat, as does the length of the moist chill period and the optimum date for seedling emergence in spring. Antelope bitterbrush seeds collected from different habitats would thus be expected to exhibit differences in seed germination response.

Previous efforts to correlate between-source differences in germination response with habitat characteristics have been successful for rubber rabbitbrush (Chrysothamnus nauseosus) and big sagebrush (Artemisia tridentata), both autumn-ripening species with little seed dormancy (McArthur and others 1987; Meyer and Monsen in preparation). Similar efforts with antelope bitterbrush have not yielded clear patterns (Meyer and others 1987a, 1987b).

ANTELOPE BITTERBRUSH SEED DORMANCY

Bitterbrush seeds have a short chilling requirement compared with seeds of other woody Rosaceae (Schopmeyer 1974). A prechill of 4-6 weeks at 2-5 °C will break dormancy in seeds from most sources (McConnell 1960; McHenry and Jensen 1967; Meyer and others 1986, 1987b; Young and Evans 1976). The required period is shortened with increasing temperature up to 5 °C; higher temperatures are largely ineffective with no dormancy-breaking effect at 10 °C (Young and Evans 1976).

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Unlike seeds of many of its rosaceous relatives, antelope bitterbrush seeds exhibit virtually no embryo dormancy. Embryos are easily excised from imbibed seeds and germinate readily and normally as long as moisture is not limiting and the embryos are kept in darkness (Hormay 1943; Meyer unpublished data; Nord 1956). This implies that the dormancy of intact seeds is somehow imposed by the thick, fibrous testa and/or the membranous endosperm.

The role of the testa or seed coat in imposing dormancy does not involve any barrier to the entry of water; seeds imbibe fully in a few hours. A possible effect of the coat is to restrict the entry of oxygen. Young and Evans (1976) invoked the oxygen-trap theory of the French physiologists Côme and Tissaoui (1973) in explaining the bitterbrush seed coat effect. They speculated that the coat might contain phenolic compounds with a high affinity for oxygen. Under warm, moist conditions, the enzymatically regulated oxygen-trapping system would combine with the low solubility of oxygen in warm water to severely limit oxygen flux to the embryo. Under moist chilling conditions, the trapping system would operate more slowly, while more oxygen would be initially dissolved in the water, so that the net oxygen flux to the embryo would be increased.

For an oxygen-trapping mechanism to impose dormancy effectively, the embryo must have an oxygen requirement in excess of that necessary for germination of a nondormant embryo. This is because nondormant embryos in general have very low oxygen requirements for germination, requirements that could be satisfied even with the trapping mechanism in place (Bewley and Black 1982; Edwards 1973). In work with charlock, an embryo-level inhibitor whose build-up was promoted by low oxygen levels was postulated to explain a similar effect (Edwards 1968, 1969).

The presence of both a chemical inhibitor and potentially oxidizable phenolic compounds has been demonstrated in seeds of antelope bitterbrush (Dreyer and Trousdale 1978). The extract containing the chemical inhibitor, which was not successfully identified, gradually lost its inhibitory activity when exposed to air. This suggests that it could be deactivated much more quickly through enzyme-mediated oxidation reactions in the embryo under conditions of adequate oxygen supply. Unfortunately, the inhibitory activity of the extract was bioassayed using lettuce seed; its activity with regard to bitterbrush embryos was not demonstrated.

If the two-step system described above is correct, it could explain why excised embryos germinate readily, but embryos in intact seeds behave as if dormant. Excised embryos have access to abundant oxygen that would rapidly deactivate an embryo-level inhibitor.

Another method for germinating dormant bitterbrush seeds without chilling is prolonged leaching in aerated water. Seeds exposed to this treatment germinate in the water in 1 to 2 weeks (K. Jorgensen personal communication). This treatment

may work by leaching an inhibitor, but its location within the seed is not known.

Hydrogen peroxide has also been used to break bitterbrush seed dormancy (Everett and Meeuwig 1978; Young and Evans 1981). It is also effective in breaking dormancy of many conifer seeds (Ching and Parker 1958; Riffle and Springfield 1968; Shearer and Tackle 1960). The efficacy of hydrogen peroxide may be due to its participation in coat oxygen-trapping reactions. In rice, the level of the enzyme peroxidase in the dormancy-imposing structure (the hull) has been correlated with the degree of seed dormancy (Navasero and others 1975). Peroxidase apparently functions in conjunction with endogenously produced peroxide in the oxidation of oxygen-sink compounds (White and others 1964). If a similar system functions in bitterbrush, hydrogen peroxide could saturate the sink compounds and slow or stop the funnelling of oxygen into the trapping system. Coat oxygen-trapping mechanisms have also been demonstrated in beets, in species of *Chenopodium*, and in other woody Rosaceae (Côme 1967; Coumans and others 1976; Dorne 1981; Heydecker and others 1971).

Dormancy-breaking chemicals that probably function at the embryo level include thiourea and gibberellic acid. Thiourea has been used as a seed pretreatment of field-sown bitterbrush seed (Everett and Meeuwig 1978; Neal and Sanderson 1975; Pearson 1957; Young and Evans 1981). Its mechanism of action is presently unknown, though it may function in some way to block an embryo-level inhibitor or interfere with its generation (Bewley and Black 1982). Much less work has been done on the effects of gibberellic acid in bitterbrush. The results of McConnell (1960) suggest that it can interact synergistically to shorten the required prechill period, but cannot replace prechill entirely.

In the present study, we looked at the interaction between prechill requirements and seed pretreatments, including soaking in water and hydrogen peroxide, as a function of seed source. We examined the effects of short-term dry-afterripening on the prechill requirement for various accessions. The effects of interruption of the prechill period with warm interruptions of various durations were also investigated.

MATERIALS AND METHODS

Seed collection was carried out during the summer of 1986 by the authors and by cooperators in various parts of the West (table 1). The fruits were hand rubbed on a rubbing board to remove the pericarps and cleaned in a table model fanning mill that removed most of the shrivelled seed. The cleaned seed was stored in manila packets under laboratory conditions until use. Only intact, nonshrivelled seeds with no visible insect damage were used.

Experiments were initiated in September 1986. Initial viability for each lot was estimated on

Table 1--Collection locations for antelope bitterbrush seed collections used in experiments. Sources followed by an asterisk were included in the 13-accession March 1987 experiment

Seed source		Lat.	Long.	Alt.
Crater's Moon	ID*	43°30' N.	113°33' W.	5500'
Hagerman	ID	42°46' N.	114°53' W.	2950'
Idaho City	ID	43°50' N.	115°50' W.	4000'
Lucky Peak	ID	43°37' N.	115°59' W.	2900'
Middleton	ID	43°49' N.	116°40' W.	2500'
More's Creek	ID	43°39' N.	115°48' W.	3200'
Reynolds Creek	ID*	43°07' N.	116°46' W.	4900'
St. Anthony	ID*	44°03' N.	111°57' W.	5800'
Wells	NV*	41°07' N.	114°48' W.	6000'
Celilo	OR*	45°38' N.	120°58' W.	400'
Eagle Creek	OR	44°52' N.	117°14' W.	2900'
Halfway	OR	44°50' N.	117°06' W.	3050'
Keating	OR	44°51' N.	117°28' W.	2800'
Mitchell	OR	44°34' N.	120°10' W.	3000'
Cottonwood Creek	UT	40°30' N.	110°12' W.	7700'
Diamond Mountain	UT*	40°37' N.	109°22' W.	7200'
Fountain Green	UT*	39°37' N.	111°37' W.	6000'
Grouse Creek	UT	40°32' N.	109°53' W.	7500'
Mosby Canyon	UT	40°34' N.	109°48' W.	7600'
Mt. Pleasant	UT*	39°32' N.	111°24' W.	6400'
Mountain Dell	UT*	40°47' N.	111°42' W.	5800'
Nephi Ridge	UT	39°21' N.	111°55' W.	5400'
Panguitch Creek	UT	37°46' N.	112°30' W.	7800'
Panguitch Lake	UT*	37°42' N.	112°37' W.	8400'
Red Canyon	UT*	37°43' N.	112°16' W.	7900'
Scofield	UT*	39°52' N.	111°07' W.	7800'
West Fairview	UT	39°37' N.	111°29' W.	6000'
Wenatchee	WA*	47°25' N.	120°17' W.	650'

four replications of 25 seeds using tetrazolium staining techniques (Grabe 1972). The seeds were first imbibed for 12 hours on germination blotters at room temperature (about 22 °C). The embryos were then excised by cutting the seed coat and the endosperm at the cotyledon end and applying firm pressure to the radicle end with thumb and forefinger. The embryos were placed in 1 percent tetrazolium chloride solution for 12 hours. Embryos stained completely red or with only minor unstained patches on the cotyledons were classed as viable. The viability estimates thus obtained are highly correlated with germination percentages for adequately prechilled bitterbrush seeds (Meyer and others 1986).

Completely randomized designs were used for all experiments. For each seed collection, four replications of 25 seeds were used per treatment. The seeds were placed between standard blue germination blotters in 100 mm plastic petri dishes and incubated in the dark. Germination tests were carried out at 15 °C for a period of 4 weeks. Blotters were moistened with tapwater as needed. Prechill treatments were carried out in the dark at 2 °C; seeds were prechilled and germinated in the same petri dishes. Seeds were considered germinated when the radicles extended at least 5 mm or showed a definite geotropic response. Germinated seeds were counted and removed at least weekly.

The first experiment tested the effect of postharvest storage period (seed age) on germination response to a 2-week prechill. All 28 seed accessions were subjected to this treatment in September 1986, after a mean post-harvest period of 2 months, and again in May 1987, after a mean postharvest period of 10 months.

In February 1987, seeds from three sources (Celilo, OR, Reynolds Creek, ID, and Red Canyon, UT) were subjected to a factorial combination of hydrogen peroxide soaking concentrations and soaking times. Concentrations included 0 (water control), 1, 3, and 10 percent; time periods were 1, 6, and 24 hours. Dry seeds were placed in beakers containing the peroxide solutions and left to stand for the indicated period of time. They were then rinsed several times with tap water and transferred directly to petri dishes while still fully imbibed.

In March 1987, seeds from 13 sources (see table 1) were subjected to an experiment that included 13 treatments. Prechill periods of 0, 2, 4, and 6 weeks were combined factorially with two presoak treatments, with and without a 24-hour standing water presoak. In addition, a 6-hour 1 percent peroxide presoak was combined with 0-week and 2-week prechill. The final three treatments involved interrupting a 4-week prechill period with a period at 15 °C after the first 2 weeks; periods of interruption were 1, 4, and 7 days.

To determine whether the peroxide treatment affected seed viability, seeds remaining at the end of the germination period in the 2-week prechill peroxide treatment were subjected to tetrazolium staining as described above. This procedure was also employed at the end of 6-week prechill treatments, as a check for dormant seeds.

Analysis of variance techniques were used to analyze experimental results. Data were arcsine transformed prior to analysis, but untransformed means are used in the data presentation. In the seed age experiment, the tetrazolium viability estimates were used to convert the results to a percentage of viable seed basis for each collection prior to analysis. In the 13-accession experiment, the tetrazolium viability data were included in the analysis as a control treatment. The Student-Newman-Keuls means separation test was used to evaluate the significance of differences between means in each experiment.

Linear regression techniques were used to analyze the relationships between treatments on a by-source basis. Data used for regression analysis were converted to a percentage of viable seed basis to minimize the effects of source differences in total viability.

RESULTS

Prechill Requirement

In general, the prechill requirement of 8-month-old bitterbrush seed was completely satisfied by 6 weeks at 2 °C (fig. 1). Only one source (Celilo, OR) had more than 2 percent dormant seed remaining at the end of this treatment.

Germination response to the 4-week prechill was significantly lower than the response to the 6-week prechill, averaging 88 percent of viable seed. Four-week prechill response also showed more between-population variation. The absolute percent increase in germination with an increase from 4 to 6 weeks of prechill varied from nil for the Red Canyon, UT, seed to 23 percent for the Celilo, OR, seed.

Germination response to a 2-week prechill averaged 43 percent of viable seed and showed the widest between-population variation of any prechill treatment, ranging from 18 percent of viable seed (Celilo, OR) to 78 percent of viable seed (Red Canyon, UT). Response to the no-prechill control treatment was uniformly low, averaging approximately 2 percent and no higher than 5 percent of viable seed from any source.

Presoak by Prechill Interaction

A 24-hour water presoak significantly increased the germination of nonchilled seeds, but mean germination percentage for this treatment was still only 11 percent of viable seed, with a maximum of 24 percent for seed from the Red Canyon, UT, source (fig 1).

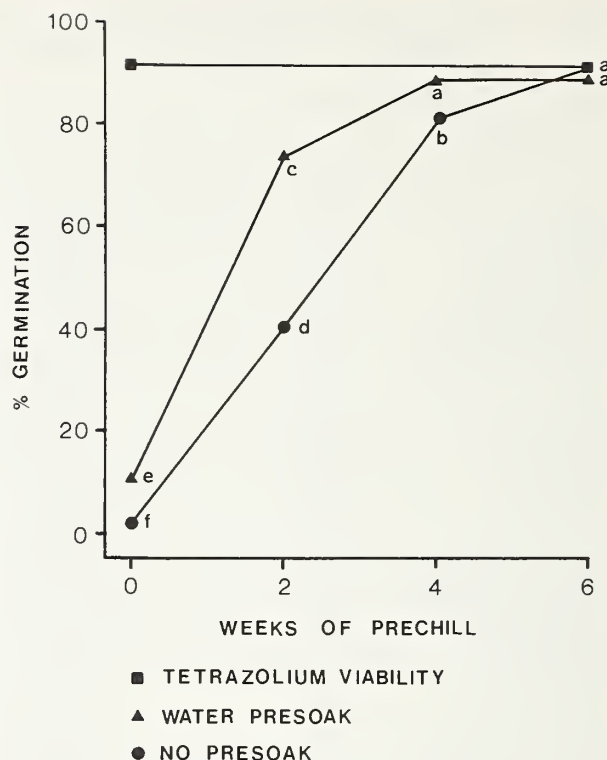


Figure 1--Mean germination response of 8-month-old antelope bitterbrush seed from 13 sources to a factorial combination of soaking and prechill treatments. The horizontal line across the top of the graph represents mean total viability, as determined by a tetrazolium test on a separate subplot of each seed collection. Points followed by the same letter have values not significantly different at the $p < 0.05$ level.

Water presoak interacted synergistically with the 2-week prechill, nearly doubling mean percentage germination over the no-soak 2-week prechill treatment (fig. 1). This treatment gave a response statistically equivalent to total viability for seed from the least dormant Red Canyon, UT, source and approached the no-presoak 4-week prechill response for seed from most sources.

Presoak had a significant effect on response to a 4-week prechill (fig. 1). Presoaked seeds germinated to full viability after a 4-week prechill, while unsoaked seeds showed a significant increase in response when prechill was increased from 4 to 6 weeks.

Results of the factorial combination of water presoak and prechill treatments show that a water presoak as applied in this experiment can reduce the prechill requirement significantly but cannot effectively substitute for prechill. It has no effect on the germination of adequately prechilled seed.

Table 2--Germination response of antelope bitterbrush seeds from three sources to a factorial treatment of hydrogen peroxide soaking concentrations and soaking times

Source	Concentration (%)	Germination percentage		
		Soaking time (hours)		
		2	6	24
Three-source mean	0	5.7	7.3	13.7
	1	34.7	57.3*	41.7
	3	56.0*	61.7*	9.3
	10	62.0	11.7	1.6
Red Canyon, UT	0	10	18	26
	1	43	72*	42
	3	69*	78*	22
	10	75*	31	5
Reynolds Creek, ID	0	4	3	6
	1	29	48	50
	3	54*	69*	6
	10	74*	4	0
Celilo, OR	0	3	1	9
	1	32*	52*	33*
	3	45*	38*	0
	10	37*	0	0

¹ Within each source, means followed by an asterisk are not significantly different from the maximum at the $p < 0.05$ level.

Effects of Hydrogen Peroxide.

Hydrogen Peroxide did not break dormancy completely in any of the seeds from the three sources tested in the soaking concentration-soaking time factorial (table 2). All accessions showed a similar pattern of response, with short to medium durations and medium to high concentrations producing the highest germination percentages. Lengthening the soak period produced a corresponding increase in germination over 24 hours only for the water control. The drop in germination once the optimum period had been reached was increasingly precipitous at higher concentrations. These results suggest that the dormancy-breaking action of the peroxide is accompanied by processes that render the embryo itself less able to germinate, not really a surprising result considering the caustic nature of the compound. These negative actions were sometimes evident as radicle-tip necrosis in the germinated seeds, a symptom not noted in the water controls. The magnitude of the response to peroxide varied; the Red Canyon, UT, seeds were much more responsive than the Celilo, OR, seeds.

Peroxide was also much more effective than a water presoak in breaking the dormancy of unchilled seeds in the 13-accession experiment (table 3). When the seeds were prechilled for 2 weeks after the soak treatments, however, the water presoak and peroxide presoak treatments were comparable.

Table 3--Mean germination response of seeds from 13 antelope bitterbrush sources to a factorial combination of presoak and prechill treatments, compared with initial viability

Treatment	Mean germination percentage
Initial viability	¹ 91.5a
No prechill	
No presoak	1.8f
Water presoak	10.0e
Peroxide presoak	41.3d
Two-week prechill	
No presoak	39.5d
Water presoak	74.1b
Peroxide presoak	
Germinated seeds	70.1c
Germinated + dormant seeds	88.5a

¹ Means followed by the same letter are not significantly different at the $p < 0.05$ level.

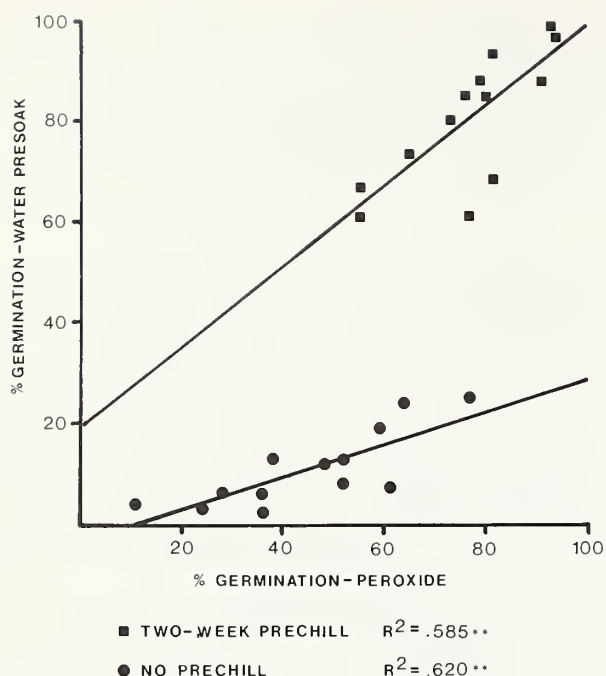


Figure 2--The relationship between germination response to a 24-hour water soak and germination response to a 6-hour 1 percent peroxide soak with no prechill (lower regression line), and after 2 weeks of prechill (upper regression line) for antelope bitterbrush seed from 13 sources.

This was not due to any negative effect of the peroxide on the viability of the remaining seeds, since the sum of germinated and dormant seeds in this treatment was equivalent to initial viability.

When the water and peroxide presoak treatments are compared on a source-by-source basis, it is evident that accessions that respond well to peroxide also tend to respond well to water presoak, resulting in a significant linear relationship between the two treatment variables both in the no-prechill control and after 2 weeks of prechill (fig. 2).

Effects of Seed Age on the Prechill Requirement

Postharvest storage period had a significant effect on the germination response to a 2-week prechill (table 4). In the 28-accession experiment an increase in seed age from 2 months to 10 months resulted in a mean germination increase from 12.5 to 35.5 percent of viable seed. When data from the 2-week prechill treatment in the March experiment are compared with data from the September and May experiments for the same 13 accessions, a significant increase in germination response with a increase from 8 to 10 months in storage is evident. These results show that short-term afterripening at room temperature can affect the degree of dormancy of antelope bitterbrush seeds.

Table 4--Germination response to a 2-week prechill as a function of seed age (storage period). Results are averaged across collections for each group and based on relative germination percentages (percent of viable seed) for each accession

Experiment	Relative germination percentage
28 Collections--1986 seed	
Mean seed age--2 months	¹ 12.5b
Mean seed age--10 months	35.5a
13 Collections--1986 seed	
Mean seed age--2 months	13.5c
Mean seed age--8 months	30.7b
Mean seed age--10 months	37.9a

¹Within each group, means followed by the same letter are not significantly different at the $p < 0.05$ level.

When germination percentages after 2 months and after 10 months of storage are compared on a source-by-source basis, it is evident that accessions that were least dormant at 2 months tended to be least dormant at 10 months, resulting in a significant linear relationship between the two variables (fig. 3). The rate of dry-afterripening of more dormant seedlots was highly variable, however. The Middleton, ID, seedlot did not respond at all to a 2-week prechill at 2 months and showed no increase at 10 months. In contrast, the Panguitch Lake, UT, seedlot showed an increase in germination response from 5 to 47 percent of viable seed over the same storage period.

Effects of Interrupted Prechill

Seed subjected to a 4-week prechill interrupted after 2 weeks by a period of 7 days at 15 °C showed an absolute decrease of about 30 percent in total germination compared with the 4-week uninterrupted prechill control (table 5). A similar effect was achieved with a 4-day mid-prechill interruption, while germination after a 1-day interruption was not significantly different from the uninterrupted control. In the 4-day and 7-day interruption treatments, the additional 2 weeks of prechilling produced an average of only a 10 percent absolute increase in germination over the 2-week prechill, while in the no-interruption 4-week control, the increase over a 2-week prechill was over 40 percent. These results suggest that the seeds left ungerminated after the 4-day and 7-day interruptions had undergone a process while imbibed at 15 °C that increased their level of dormancy.

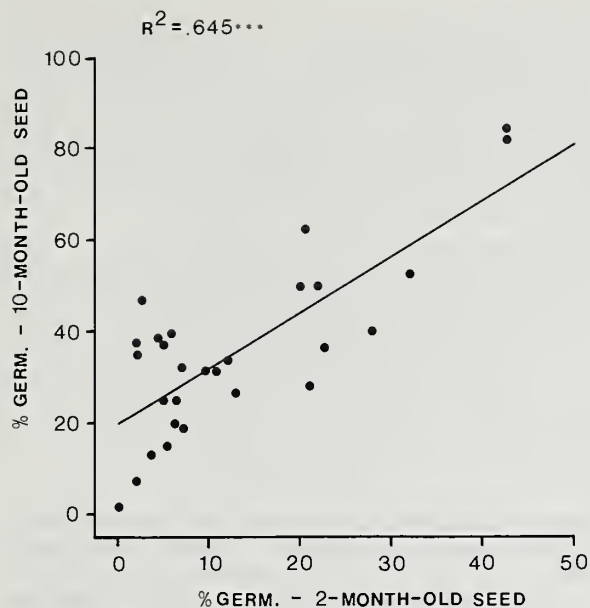


Figure 3--The relationship between the germination response of 2-month-old seed and that of 10-month-old seed to a 2-week prechill treatment. Results are expressed on a percentage of viable seed basis for each of the 28 seed collections.

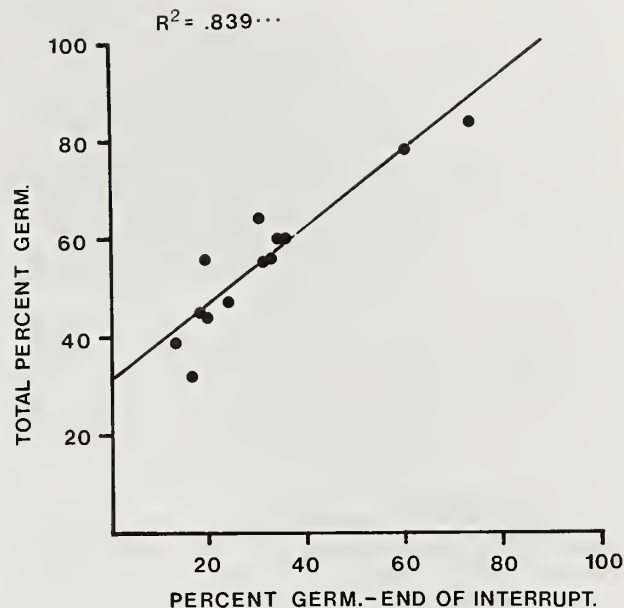


Figure 4--The relationship between germination percentage at the end of the 7-day interruption and total germination at the end of the final germination period for the 4-week 7-day interrupted prechill treatment. Values for each of the 13 seed collections are expressed as a percentage of viable seed.

Table 5--Mean germination response of seeds from 13 antelope bitterbrush sources to a series of prechill and interrupted prechill treatments. Interruptions followed the first 2 weeks of 4-week prechill periods

Treatment	percentage
4-week prechill	
No interruption	¹ 81.4a
1-day interruption	82.7a
4-day interruption	52.8b
7-day interruption	51.5b
2-week prechill	39.5c

¹Means followed by the same letter are not significantly different at the $p < 0.05$ level.

Many of the seeds that germinated in the 4-week 7-day interrupted prechill in fact germinated during the interruption, and the total number of seeds germinating at the end of the test was closely correlated with the number that germinated during the interruption period (fig. 4). If we consider only viable seeds remaining at the end of the second 2 weeks of prechill, we see that from 17 to 49 percent of these seeds germinated, with an average of 37.2.5 percent (mean \pm standard error). No clear trends are evident on a source-by-source basis. The warm interruption effectively induced secondary dormancy (increased dormancy) in still-dormant seeds of all sources.

DISCUSSION

The required prechill period reported here (4-6 weeks) agrees well with earlier values reported for antelope bitterbrush (Young and Evans 1981). Considering the range of site types over which collections in this study were made, there was relatively little between-source variation in the prechill requirement, and this variation was not correlated in any obvious way with site conditions.

These results are in contrast to those reported for some other woody Rosaceae. In wild pear species, length of required prechill was positively correlated with the length and severity of the winter at the site of seed collection (Westwood and Bjornstad 1968). In almond varieties, the length of the prechill required to break seed dormancy was positively correlated with the prechill required to break bud dormancy (Kester 1969). This in turn was related to the provenance of the variety. In both pear and almond, control seems to be at least partly genetic and to reside at the embryo level, since crosses of long-seed-prechill plants with short-seed-prechill plants generally produce seeds with intermediate prechill requirements in a common garden. In rose cultivars, the length of the prechill requirement was strongly affected by year-to-year variation in common garden conditions during the latter stages of seed maturation (Von Abrams and Hand 1956). Seed ripened at warmer temperatures was less dormant than seed ripened at cooler temperatures. There are apparently genetic differences in the prechill requirements of different rose species as well (Densmore and Zasada 1977; Semeniuk and Stewart 1962; Svejda and Poapst 1972). In bitterbrush, no clear trends in the effect of genotype or of predispersal environment on prechill requirement have emerged.

Shortening or eliminating the prechill requirement with a water presoak has been effective for many species (Barton 1954; Janerette 1979). The usual explanation is the leaching of an embryo-level or seed-coat level inhibitor, though this has only sometimes been rigorously demonstrated (Bewley and Black 1982). The presoak treatment used here was not sufficient to substitute for prechill, but it may have lowered the level of some inhibitor, possibly at the embryo level, to a point that approached a threshold level. It thus interacted synergistically with a 2-week prechill to produce germination percentages that greatly exceeded the sum for the two treatments separately.

The hydrogen peroxide treatment, unlike the water presoak, was able to substitute for prechill to a substantial degree. It may work by oxidizing coat level phenolics that are not readily leached with water. Its interaction with a 2-week prechill was essentially additive, which suggests that it works by a different mechanism than the water presoak. The fact that accession response to peroxide was highly correlated with response to water presoak may indicate that accession differences are due to differences in embryo inhibitor levels. Seeds with lower levels would be brought closer to a threshold level by soaking. They would also require less oxygen for deactivation and would thus respond more positively at a given level of immobilization of a coat oxygen trap.

The reduction of seed dormancy as a consequence of dry storage has been observed in a wide range of species, but the mechanisms remain largely unknown (Bewley and Black 1982). The effect may be to increase the range of conditions over which germination may take place, to make possible the

germination of previously dormant seeds, or, as in the case of bitterbrush, to shorten the period of pretreatment necessary to permit germination of previously dormant seeds. The rate of dry-afterripening is temperature dependent and may be much accelerated at higher temperatures for some species (Bewley and Black 1982; Capon and Van Asdell 1967; Taylorson and Brown 1977). The storage temperature used in this study (20 °C) was probably not high enough for maximum rates of afterripening and certainly did not approach summer temperatures likely to be experienced by bitterbrush seeds in the field (Ferguson 1972), or even in uncontrolled warehouse storage. The effect of high temperature on the rate and degree of dry-afterripening in antelope bitterbrush has not yet been systematically investigated.

The induction of secondary dormancy in seeds maintained imbibed under conditions not suitable for germination is also a well-known phenomenon (Bewley and Black 1982). In rosaceous shrub seeds, the degree of dormancy is often increased at temperatures above a certain threshold value and decreased at temperatures below it. At the threshold or compensating temperature, no change in dormancy takes place (Bulard 1985; Kester 1969; Stewart and Semeniuk 1965). The threshold value varies from species to species and even among accessions of the same species. The dormancy-breaking process is thus reversible, and interruptions in the prechill period produce essentially the same result as that reported here for bitterbrush, an increase in the prechill requirement of the remaining ungerminated seeds. The observations made here are consistent with the idea of an embryo-level inhibitor whose production or efficacy is enhanced at low oxygen levels, since the oxygen level in the interior of the intact seed is much decreased at higher temperatures. A further implication is that the prechill requirement of a seedlot could be increased by imbibing the seeds at warm temperatures prior to the initiation of any prechill. Preliminary data (Meyer and Monsen in preparation) support this possibility for bitterbrush.

The evidence presented here is congruent with a seedcoat oxygen trap-oxidizable inhibitor model for bitterbrush seed dormancy, but it by no means presents rigorous proof for such a model. Much more detailed work at the physiological level will be necessary before the processes involved can be fully understood.

The intuitive idea that bitterbrush seed collections from sites with long, severe winters will have a longer prechill requirement than collections from sites with short, mild winters was not supported by the 13-accession study. All 13 accessions had requirements of 6 weeks or less, and only one (Red Canyon) was rendered largely germinable by a treatment of less than 4 weeks.

In the 28-accession, fresh seed, 2-week prechill experiment, the least dormant sources were mostly high-elevation sources from central and southern

Utah, while most of the strongly dormant sources were from low elevations on the Snake River Plains and the Columbia Plateau of Idaho and Oregon. This trend was not without exceptions, but it was strong enough to prompt an attempt at interpretation. Results of the afterripening and interrupted prechill experiments may provide clues to a possible explanation.

Seeds of low-elevation northern sources ripen early in the summer and are exposed to a long period of warm, dry conditions prior to the onset of prechill. If dry-afterripening is accelerated at high temperatures, these seeds could become susceptible to germination during the hazardous fall period after rains have begun but before the severe frosts of winter. They may need to be strongly dormant initially to avoid afterripening too much during the dry summer.

Seeds of high-elevation southern sources, on the other hand, ripen late in the summer. But summers are moist, and these seeds would be exposed to warm, moist conditions after dispersal. Such conditions may be effective in increasing their prechill requirement to such a degree that it might not be satisfied by the on-site winter prechill duration. Such seeds would increase their chances of survival if dispersed in a relatively nondormant state, providing that they are completely dormant under the conditions of the summer-moist pretreatment itself.

Even if all seed from all sources started out with a similar degree of dormancy, experiences after dispersal would tend to condition them for the prechill period likely to be encountered at their respective sites. Seeds from sites with hot, dry summers and short, mild winters would tend to become less dormant after dispersal through dry-afterripening. Seeds from sites with warm, moist summers and long, cold winters would tend to become more dormant after dispersal because of dormancy-deepening processes that may operate on imbibed seeds at warm temperatures.

The data presented here are not sufficient to demonstrate an ecological relationship between seed characteristics and site characteristics that affect seeds after dispersal. These ideas represent working hypotheses that are currently under continuing investigation using both laboratory and field burial techniques.

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FIRE EFFECTS ON AMELANCHIER ALNIFOLIA SHRUBS DURING PHENOLOGICAL DEVELOPMENT STAGES //

Nonan V. Noste, Elizabeth D. Reinhardt, and Ralph A. Wilson, Jr.

ABSTRACT: Artificial fuel beds were used to burn serviceberry shrubs with fires of known duration and intensity. Plants burned early and late during the growing season resprouted slightly better than those burned in midseason. Sprouting response was related to size of the plant, but not to ratio of dead/live stems. Plant response did not vary significantly between fire treatments. The relationships between fire treatment, fire behavior, and the heat pulse to the plant and site are discussed.

INTRODUCTION

Fire is a natural process in forest communities of western Montana and throughout the West. Wildfire has historically played a role in the succession of plant communities that contain intolerant shrubs as a seral component. Strategies to manage sites that contain intolerant shrubs include the use of prescribed fire.

Prescribed fire provides managers with a cost effective method of manipulating plant communities to increase resource production. Old decadent shrubs may produce little annual growth, and the younger more succulent plant parts may be out of reach of even large ungulates. Burning these shrubs to kill above-ground stems should result in an increase of young available sprouts from underground buds, increasing both wildlife browse production and availability.

To use prescribed fire effectively, we need to understand the relationships between fire treatment and fire effects. The effects of season, fire characteristics, and preburn plant characteristics on plant response need to be quantified to determine what time of year and type of fire best achieve above-ground stem mortality without removing the plants from the site. Opportunities for prescribed burning may be limited by lack of fuel. Natural fuel loadings may be inadequate to produce a fire that spreads through the area and is intense enough to kill the above-ground stems.

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Fire applied at different times of the year may produce varying shrub response. Seasonal differences in shrub response may be due to changes in plant carbohydrate reserves. They may also be due to changes in soil moisture, which affects thermal conductivity and thus the transfer of heat to underground plant parts. Understanding seasonal variations in plant susceptibility to fire will aid in development of fire prescriptions that can best meet management objectives.

Burning during the season of active growth resulted in increased mortality of shrubs in the northern Sierra Nevada (Kaufman and Martin 1985). Miller (1977) found that more rhizomes of huckleberry (*Vaccinium globulare*) survived spring fires than more severe fall fires; however, there was no seasonal difference in sprouting rate of those rhizomes that survived.

The inability to characterize and control the heat pulse to the plant has sometimes been an obstacle to understanding the seasonal response of shrubs to fire, making it difficult to separate the effects of season from the effects of fire treatment. Flinn and Pringle (1983) used water baths for heat treating eight shrub species to control the temperature and duration of the treatment. They documented seasonal variation in sprouting rates following these treatments.

Shrub response to fire may also vary with fire severity. Fire severity depends on the heat pulse up to the plant, as indicated by flame length, and heat pulse downward to the soil, as a result of burnout of ground fuels (Ryan and Noste 1985). Rhizomes subjected to nonlethal heat treatments showed increased sprouting over untreated rhizomes (Flinn and Pringle 1983). Excessive heat (usually temperatures over 55 or 60 °C) resulted in rhizome mortality. Johnston and Woodard (1985) studied the effect of fire severity on hazel (*Corylus cornuta* Marsh.) and raspberry (*Rubus strigosus* Michx.) by artificially adjusting fuel loads on small plots within a single large burn. They found that above-ground plant parts were killed even by low severity fires. They found some below-ground mortality under plots with heavy fuel loads.

The objectives of this study were to examine the effects of season and severity of fire treatment on sprouting response of one species, Saskatoon serviceberry (*Amelanchier alnifolia* Nutt.). Serviceberry is often an important winter food source for whitetail deer, mule deer, elk, bighorn sheep, mountain goats, and moose (Hemmer 1975). It has been characterized as relatively high in fire survival capability due to its massive rooting system, which is rhizomatous and deeply

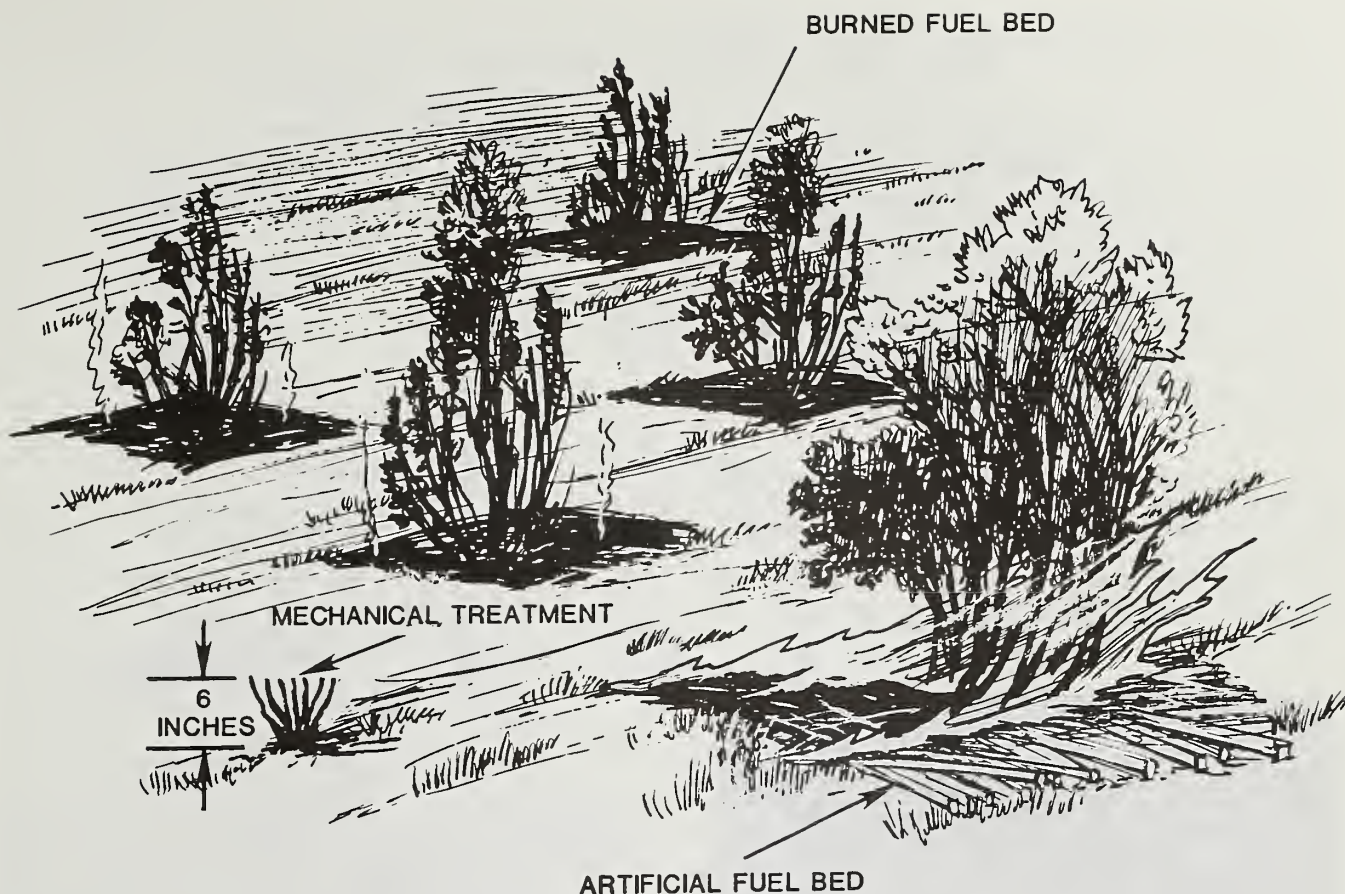


Figure 1--Plot layout showing one group of shrubs receiving the six treatments.

placed (Bradley 1984). In a study contrasting the ability of a spring and a fall prescribed burn to improve wildlife habitat, a severe fall treatment killed 15 percent of the serviceberry plants on the site, while a less severe spring treatment killed only 5 percent (Noste 1982). Sprouting response in the first 2 years following the fire was greater on the spring burn.

METHODS

Saskatoon serviceberry plants in a Douglas-fir/snowberry (*Pseudotsuga menziesii*/*symphoricarpos albus*) (Pfister and others 1977) habitat type north of the Ninemile Ranger Station in the Lolo National Forest in western Montana were burned in 1984 and 1985, using artificial fuel beds to produce high and low intensity, long and short duration fires by manipulating loading and fuel particle size. Heat pulses to the soil and stems were measured to characterize the treatment from these fuels.

Individual serviceberry shrubs were treated with fire during four different phenological stages. Selected plants were mature, growing in an open stand condition on relatively level ground, and not heavily browsed. Twelve groups of six plants each were used to provide three replicates of six treatments during four phenological stages of plant development:

1. Before leaf bud burst.
2. After leaves were fully developed.
3. After initial change in fruit color.
4. After first leaf coloring in fall.

The six treatments were randomly assigned to the six plants in each group (fig. 1). Five of the treatments were designed to provide a range of fire intensity and duration commonly found under natural conditions, while the sixth treatment was mechanical removal of above-ground stems:

Treatment	Fuel load	Surface/ volume	Diameter
Severity duration/	T/ac	kg/m ²	l/cm in.
1 mod-mod	5	1	6 1/8-1/4
2 light-mod	2	0.4	6 "
3 heavy-mod	10	2	6 "
4 mod-fast	5	1	81 excelsior
5 mod-slow	5	1	3 1/2
6 clipped	-	-	-

Plants were measured before treatment to determine their size and condition. All stems within 0.5 m of the plant center were tallied by diameter class, height, and status (live or dead). Biomass

was computed using Brown's (1976) equations. Ratio of live to dead stems was used as an indicator of plant vigor.

The plants were instrumented with thermocouples to quantify the heat treatment they received. Three stems on each shrub were instrumented with two thermocouples 10 cm above the ground, one taped to the bark surface, and another installed 2 mm underneath it, approximately at the cambium layer. This allowed documentation of the temperature gradient through the bark to the cambium. A set of four thermocouples was used to monitor heat movement into the soil. These were placed at the soil surface and 1, 3, and 5 cm below the soil surface.

Fuels were conditioned to approximately 6 percent moisture content by storing them indoors. Litter and dead stems were removed from a 2 by 2-meter area around each shrub prior to building the artificial fuel bed. This area was then uniformly covered with the conditioned fuels (fig. 2).

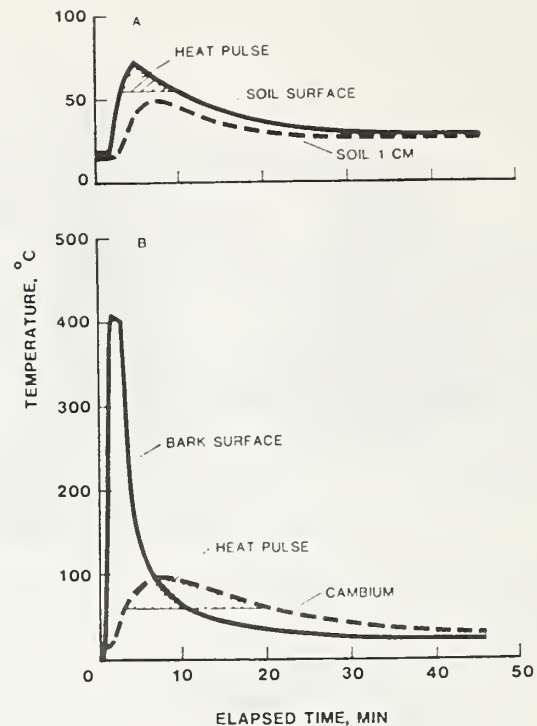


Figure 2--A serviceberry shrub receiving treatment 1.

Fires were ignited along the downslope-down-wind edge of the fuel bed. Rate-of-spread was timed between metal stakes spaced at 1/2-meter intervals from a stake at the plant center. Flame length and depth were recorded at each stake. Temperature, windspeed, and relative humidity were observed at the time of the burn using a belt weather kit.

Temperatures during the burn were monitored at 30-second intervals and recorded electronically, using a Campbell Scientific CR5 digital recorder. A typical temperature profile is displayed in figure 3.

Serviceberry sprouts within 0.5 m of the plant center were counted by size class at the end of one growing season after burning as a measure of treatment response.



Figures 3A and 3B--Time temperature profiles for a representative burn. Figure 3A shows profiles for thermocouples on the soil surface and 1 cm below the soil surface, while figure 3B shows profiles for the thermocouples on the stem. The shaded areas show the "heat pulse" as it was computed for each plant.

ANALYSIS

Analysis of variance was conducted using a split plot design, with post treatment number of sprouts per shrub as the dependent variable, phenological stage as the main plot, and fire and clipping treatment as subplots. The preburn size of the shrub and ratio of dead-to-live stems were added as covariates to increase the sensitivity of the test. Post treatment sprout biomass was also used as a dependent variable. Because results were parallel, only number of sprouts will be reported.

Total heat release was computed from fuel heat content, fuel loading, rate of spread, fuel bed depth, and residence time (Rothermel 1972). The temperature profiles were used to compute a heat pulse to the cambium and the 1 cm depth in the soil. Heat pulse was defined as the area under the time temperature profile curve but above 60 °C. Fire behavior and heat pulse were summarized for descriptive purposes, and relationships between them were examined.

RESULTS

All fire treatments killed virtually all the above-ground plant parts. Little heat increase was observed below 1 cm depth in the soil. All plants resprouted vigorously.

Table 1--Split plot analysis of variance of serviceberry sprout response to treatment and phenological stage with ratio of dead/living stems and size of shrub as covariates

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	Probability of F
Main plot analysis					
Plant stage	3	11743	3914	6.86	0.0008
Error A (Replications within stage)	8	12056	1507	2.64	0.0209
Sub-plot analysis					
Treatments	5	2763	553	0.97	0.4495
Stage x treatment	15	14697	980	1.72	0.0891
Covariates					
Size of shrub	1	12604	12604	22.08	0.0001
Live/dead ratio	1	60	60	0.10	0.7481
Error B (Error A x treatment)	38	21688	571		
Hypotheses test using the "A" error term					
Plant stage	3	11743	3914	2.60	0.1247

No significant differences at the 90-percent confidence level were found between the five fire and one clipping treatments (table 1). Number of postburn sprouts was positively and significantly related to preburn size of the shrub. Plant sprouting response was not significantly correlated to ratio of live-to-dead stems. There was some indication that spring and fall burns encourage sprouting (tables 2a, 2b); however, the relationship between sprouting and phenological stage was not significant at $\alpha = 0.12$, and might be described as being "marginally significant."

Fire behavior and heat pulse varied significantly between the treatments (tables 3 and 4). There was a positive correlation between total heat release, and soil and stem heat pulse. There was no correlation, however, between the observed fire behavior parameters and heat pulse to the stem or soil (table 5). The relationship of soil heat pulse to stem heat pulse was insignificant with a correlation coefficient of 0.10.

DISCUSSION

The weak relationship of sprouting response to phenological season of treatment suggests that timing of burn treatment is not an important managerial concern. Similar results can be expected from spring, summer, and fall fires, although a slightly reduced sprouting response may be expected following summer treatment. This slightly reduced sprouting rate may be due to lower carbohydrate reserves in midseason, as plants expend their stored carbohydrates in leaf

Table 2a--Serviceberry sprout response for four phenological stages of plant development (n=72)

Phenological stages	Average number of sprouts/plant
Before leaf bud burst	89
After leaves are fully developed	59
Initial change in fruit color	76
First leaf coloring in fall	90

Table 2b--Serviceberry sprout response to treatment

Treatment No.	Number of sprouts/plant
1. mod-mod	88
2. light-mod	72
3. heavy-mod	75
4. mod-fast	81
5. mod-slow	81
6. clip	73
Mean	78

development and shoot elongation. Stored carbohydrates were not measured in this study, however.

All above-ground stems were killed by all five burn treatments, while rhizomes did not receive

Table 3--Fire behavior characteristics of five fire treatments

Treatment	Rate of spread m/min	Flame depth dm	Flame length dm	Residence time min	Total heat release mJ/m ²
	----- mean -----				
1	0.47	3.6	5.1	1.6	52.0
2	0.16	2.3	2.1	4.1	20.0
3	0.37	4.9	9.9	1.4	105.0
4	4.05	4.8	14.2	0.6	41.0
5	0.12	3.0	2.8	4.5	44.0
Number	68.00	68.00	68.00	68.00	69.0
F ratio	3.26	3.74	33.64	8.57	11.57
Pr >F	0.02	0.01	0.00	0.00	0.00

much heat treatment. This indicates that even low intensity fires are sufficient to top kill serviceberry plants, and that fires in natural fuels are unlikely to damage underground buds and remove plants from the site, at least for the range of conditions we tested. Evidently managers have a large window of opportunity in treating serviceberry shrubs with fire. Successful burning to top kill serviceberry shrubs seems not to be limited by a need to achieve a restricted range of fire intensities. Conditions that allow a continuous fire may be used to set the lower limit for burn prescriptions. Upper limits may be set by control constraints or constraints derived from other resource objectives. In situations where there is deep duff or large amounts of woody fuel, one might expect to see some below-ground mortality. If this is a concern, prescriptions should be set to burn when duff moistures are high.

The five fire treatment fuel loads were arbitrarily chosen to yield a range of heat pulse to the site and consequently a range of stem kill. Evidently this range was not great enough to create a range in plant response. Because sprouting did not relate to our treatments, we did not attempt to relate plant responses to fire characteristics. The fire characteristics of the five treatments may, however, be of interest in designing future studies or operational burns. Heavier loadings may cause below-ground mortality, while lighter loads of fine fuels might not kill all above-ground stems.

The fuel beds for the five fire treatments were designed by using the fire behavior model (Rothermel 1972) to identify fuel loads and sizes that would result in desired fire characteristics. These prescribed fire characteristics and those actually achieved are shown in table 6. Observed flame lengths were similar to predicted flame lengths. Actual residence times were longer than anticipated, but generally the same order of magnitude. Total heat release calculated from the observed spread rate assumes 100 percent burning efficiency, hence these values are unreasonably large, but are in excellent order with the predicted values.

Table 4--Heat pulse from five fire treatments

Treatment	Fire characteristics		
	Heat pulse Soil	Stem	Time Above 60 °C
	----- mean -----		
1	388	758	8.4
2	21	226	5.5
3	1561	667	17.2
4	88	223	10.5
5	521	577	11.2
Number	52	52	57
F ratio	2.70	4.23	1.0
Prob F	0.04	0.005	0.40

SUMMARY AND CONCLUSIONS

Response to treatment generally followed the expected pattern. Larger plants resprouted better. Resprouting was slightly less for plants burned during the growing season. Resprouting was not related to fire severity for the fuel loads tested. There was no relationship between observed fire behavior and the heat pulse to the plants.

Phenological stage had a marginal effect on sprouting response. Plants do not resprout quite as well if burned during the "leafed out" and "fruiting" stages. The reason may be low carbohydrate reserves. Study results support the practice of spring and fall burning to increase the shrub component of stands, and midseason burning to reduce shrubs, but suggest that season of burn is not an important factor in serviceberry response to fire.

The size of the shrub was positively related to sprouting response, while the proportion of dead stems in the plant was not a deterrent to resprouting. The management implication is that even decadent shrub fields may be successfully treated with fire.

Table 5--Relationship between fire behavior and heat pulse

Heat pulse	Rate of spread	Flame depth	Flame length	Residence time	Total heat release
- - - - - Correlation coefficient - - - - -					
Soil	-0.07	0.06	0.09	-0.09	0.27
Stem	-0.14	0.04	-0.02	-0.12	0.22
- - - - - Significance level - - - - -					
Soil	0.31	0.35	0.26	0.25	0.03
Stem	0.17	0.39	0.45	0.19	0.06

Table 6--Target and achieved fire treatments

Fire treatment	Flame length m		Residence time min		Total heat release mJ/m ²	
	Target	Observed	Target	Observed	Target	Observed
1	0.2-0.5	0.51	1.0	1.7	20	52
2	0.05-0.1	0.21	1.0	4.1	8	20
3	0.5-0.75	1.00	1.0	1.4	40	105
4	1.5-2.0	1.42	0.2	0.6	20	41
5	0.1-0.15	0.28	2.0	4.5	20	44

Plant response to burn treatment was insignificant. The range of fuel loadings tested resulted in fires that killed all above-ground stems but did not kill the below-ground plant parts.

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THE ECOLOGY OF VACCINIUM GLOBULARE:

SEEDLING ESTABLISHMENT AND NUTRITION //

Nellie M. Stark

ABSTRACT: Studies of the wild Montana huckleberry (Vaccinium globulare) are in progress to provide the information needed to supply the growing huckleberry industry with a stable supply of fruit. The plant provides an important food supply for wildlife as well. Seed germination in the wild is rare except in unusual years when the temperatures are favorable and when the soil remains constantly moist for a year or more. Water holding capacities of soils that exceed 22 percent are associated with better seed germination and seedling survival. Burial of the seeds by litterfall may reduce field germination. The plants normally reproduce asexually by growth of rhizomes. Container-grown seedlings provided with a special fertilizer in peat moss will produce exceptionally vigorous roots. Large plants that produce good fruit yields have more of most nutrients, including copper and boron, than large non-producing plants. High concentrations of manganese may be detrimental to fruit production. Soils supporting high fruit production in nine out of ten years had significantly more available boron, magnesium, calcium, phosphorus, zinc and total nitrogen than soils supporting plants that bear good fruit crops one out of ten years.

INTRODUCTION

The Montana wild huckleberry (Vaccinium globulare) is a fruit of considerable importance to wildlife and humans. Since the genus is Vaccinium, the plants are actually blueberries, but are called "huckleberries" in Montana in recognition of their exceptional flavor. The fruit is eagerly sought for pies, candies, jam and jellies by a rapidly growing industry.

Huckleberry plants are frequently damaged by desiccation and cold when the tops extend above shallow snow packs during winters with low precipitation, especially at low elevations. Spring frosts often destroy the flowers resulting in poor crops. Occasionally there is failure of pollination in cool and rainy springs. Summer drought is another common problem that diminishes berry

production. These natural phenomena, alone or in combination, frequently produce shortages of fruit for both industry and wildlife.

The huckleberry harvest from wild fields in western Montana exceeds 454,000 liters in good years, but may fall below 227,000 liters in poor years (Stark, unpublished). If the huckleberry industry is to continue to develop in Montana, it is essential to find ways of guaranteeing a more stable supply of fruit. Thus, extensive studies of the ecology of huckleberry have been undertaken to provide the information needed to maintain good field berry production for wildlife and human use.

Huckleberry products are being marketed from Montana over much of the United States with plans to expand to international markets. Annual income to Montana from the wild fruit exceeds several million dollars at present.

Three areas of research are being pursued to meet the growing commercial demand for fruit and lessen the adverse impacts of disturbance and diminished food supply for wildlife: the manipulation of wild berry fields to improve production for wildlife, field ecology of the species and the cultivation of berry plants for garden plantings. This paper reports results primarily from the ecological studies.

Much is known about the blueberry family (V. membranaceum, V. myrtillus, V. angustifolium), particularly the commercial blueberry species. Small (1972) described the photosynthetic strategy of bog plants, indicating a high photosynthetic efficiency for V. myrtilloides and a high nitrogen use efficiency. Factors that influence the decline phenomenon in Maine lowbush blueberries (V. angustifolium) were reported by Trevett (1956). Yarborough and others (1986) reported maximum yields of V. angustifolium in Maine of 3,926kg/ha after treatment with 1.83 kg hexazinone/ha. This treatment is presently being tried in Montana. Janke (1968) reported on the ecophysiology of V. myrtillus, emphasizing energy exchange. Pollination strategy and disease problems were described by Batra and Batra (1985), with emphasis on the mummy berry disease, Monilinia sp. Bannister (1980) reported increased winter carbohydrate losses and lower summer carbohydrate gains for species growing in cool, moist climates. High and lowbush blueberries in Michigan were studied by Pritts (1984) for yield component interactions, genetics and biomass partitioning. The ecology of

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a closely related species, *Vaccinium membranaceum*, was studied by Minore and others (1979) for populations occurring in Washington State. The nutritional requirements of the Washington populations of *V. membranaceum* were reported by Nelson in 1974 and Minore studied the tolerance of the same species to manganese in 1975. Studies of other species of *Vaccinium* from around the world have little bearing on the Montana species.

Montana has three other species of *Vaccinium* which are not presently being studied. Van der Kloet (1984) has indicated that the main berry-producing plant in Montana may actually be a large ecotype of *V. deliciosum* which grows on the Washington coast. The Montana plants are 0.3 to 0.6 m tall and bear fruit ranging in color from black to blue to red. The Montana plants are quite different in appearance to the coastal *V. deliciosum*, however. Since no verification of the name change has appeared in the literature, I use in this report the name *Vaccinium globulare*, which is currently accepted as the appropriate scientific name (Stickney 1972). This report is a summary of my progress to date. Technical details including methodology will be published next year.

REPRODUCTIVE CHARACTERISTICS

Seed Germination

Studies of the influence of temperature, pH, seed source and light on the germination of *V. globulare* seeds have indicated a strong influence of environment on seed germination. In nature, the seeds may germinate, but young plants grown from recently germinated seeds have not been found by any of a number of scientists who frequent the wild berry fields (Stickney 1985). Seed germination may be unsuccessful because of the young seedlings dependence on a constantly moist substrate. In germination tests in the laboratory, plates that became even slightly dry, especially during the early germination phase, failed to produce seedlings. Other evidence of the dependence of young seedlings on moisture came from soil transfer studies. One soil type with a high ash content and associated high water holding capacity (22 percent) supported twice as many seedlings as a soil that is typically less productive and 40 times more seedlings than a soil which supports a good berry crop once in ten years (water holding capacity of 11 percent). One of the soils had been moved from its original location so that the two soils were side by side in the same microclimate.

Seeds germinated poorly in shaded conditions where the exposure to light was less than 1 percent of full sunlight. This type of light exposure is common in the wild because the leaves of the huckleberries and those of *Alnus sinuata*, a common associate, fall in the autumn after the fruit have fallen to the ground. The result is frequent burial of the fruit and seeds which produces few, weak seedlings that are unable to grow through the autumn accumulation of litter. Overall, germination is three times better with exposure of seeds to light near to 10 percent of full sunlight than at less than 1 percent of full sun.

Surface temperatures of 5 and 30 C produced no seed germination. In spring when germination would normally occur, 5 C temperatures would not be unusual in the field. The 30 C temperature is probably not achieved during the year, except during late summer on extremely open south slopes. Temperatures of 30 C caused accelerated drying of the substrate. The best germination occurred at 20 C (70 percent) with somewhat poorer germination at 10 C (52.6 percent). Germination was reduced at higher soil temperatures. Considering that the seeds would normally germinate during a period when the soil temperatures were between 5 and 8 C, temperature could well be another factor discouraging seed germination in the field.

Good seed germination occurred at pH 4, 5, and 6, which is the normal range for spring surface soil. Soil acidity is not suspected as a factor preventing seed germination.

Fruit pulp does not appear to have any direct inhibitory effect on seed germination, except for the physical burial of the seeds. Seedlings were able to push through the pulp and emerge into the light, but at a greatly reduced rate (3 to 5 percent germination compared to 73 to 83 percent for seeds free of pulp). Burial of seeds by pulp that is not fully decomposed under the snow may account for some germination failure. Germination varies by family and year from 46 percent to 84 percent of normal appearing seeds. Plants produce up to 58 percent aborted seeds, so germination is based on the remaining 42 percent sound appearing seed. Data on wild fruit production have been limited by three years of poor crops, during which fruit production ranged from 0 to 1,600 kg/ha. Considering the extensive cover of other brushy species on the average hectare (25 to 79 percent) and the frequent poor droughty or cold years, the low production is understandable. Yarbrough and others (1986) reported 3,926 kg/ha for Maine blueberries in areas with brush control. The Maine fruit are borne in clusters and are more prolific than the Montana species which bears fruit singly. A meter square area in Montana can produce about 580 fruit of *V. globulare*. Each fruit has about 40 normal-appearing seeds with a germination potential of 42 percent (worst possible case) or a calculated ability to produce on the average 9,744 viable seeds/m². This translates to about 97,440,000 potential seedlings per hectare per year. Obviously the seed source is present, yet we did not find the seedlings in nature. Only under closely controlled conditions was it possible to obtain germination in the field. This work agrees with that of Vander Kloet (1976) who concluded that unfavorable soil temperatures and water stress were the main reasons why *V. angustifolium* was unable to produce a crop of seedlings more than once a century. Both species propagate asexually by rhizomes.

Rooting

One reason why the Montana huckleberry has not been grown commercially to date is the problem of transplanting seedlings from the field. The plants have rhizomes that grow 3 to 8 cm beneath the soil and litter. These rhizomes bear a few

fine, weak roots that are almost impossible to excavate intact. Without the roots, the rhizomes must be held in a mist chamber until they can develop new roots, a slow process with a high mortality rate. My recent studies show that the plants will grow well from seeds, although the resulting stock is widely variable in appearance. Seeds placed in a rooting medium of low bulk density, such as peat moss, grow readily and produce extensive, vigorous roots. When grown in open containers, the roots intermingle so extensively that it is difficult to transplant individual seedlings. Plants grown in "supertubes" (containers) with peat moss and a special fertilizer supplement produce exceptionally vigorous, compact roots (fig. 1). Tissue culture is presently being used to develop more genetically uniform planting stock. Once the culture methods are perfected, the sprouts will be grown in supertubes to concentrate root development.

Because of the failure of seed germination in the field, new genetic combinations are being formed naturally, but not tested frequently in nature. For this reason, we intend to continue to screen seedlings through seed germination for superior strains that may not yet occur in the field. Testing requires growing the plants in gardens until they reach bearing size. Maintenance of the flavor of the fruit is a high priority. Also, because the plants spread predominately by rhizomes at the rate of about 20 cm per year, the species has probably not reached the extent of its potential range. This is supported by field tests of planted seedlings that are surviving well beyond the species present range.

CARBON AND NUTRIENT ALLOCATION

Plants of *Vaccinium globulare* were collected from 0.1m² subplots in 35 stands covering seven major berry-producing areas in western Montana. Plants varied in size, age and fruit production, but all were from sunny locations. These plants and the soils that they grew in were analyzed for nutrients, fruit production and carbon allocation to determine what conditions appear to correlate well with good growth and berry production. The populations were

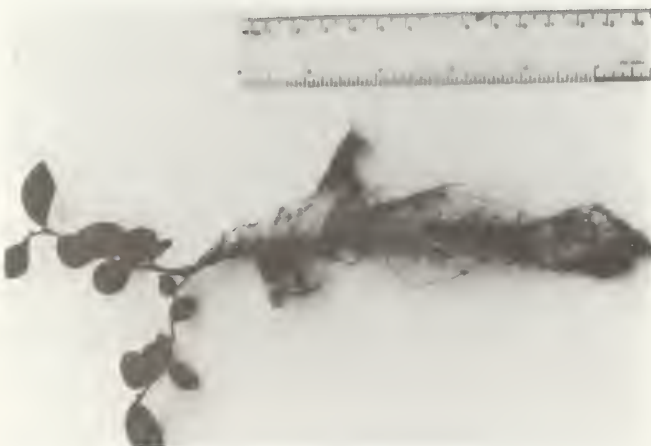


Figure 1--Photograph of root system of a seedling of *Vaccinium globulare* grown in a super tube.

divided into small plants with no fruit, large plants with no fruit (but adequate water on the site) and large plants with >40g/m² of fruit production. This allowed examination of the nutritional conditions favoring fruit production. It also allowed us to examine how the plants partition carbon into specific types of compounds through the aging process.

When data from the entire population were combined and plotted with standard deviation for each nutrient using centric polygrams (regardless of production or size), the nutrient concentrations of leaves, new stems, old stems and rhizomes had large standard deviations, as expected (Stark, in press). In general, the leaves had the highest concentrations of nutrients on a micrograms per gram basis, with new stems, old stems and rhizomes in descending order of total nutrient content. Surprisingly high concentrations of Mn occurred in the leaves, approaching 3,000 ppm, with up to 4,000 ppm Mn in the new stems. Boron concentrations were quite variable in the leaves but highly consistent in all other plant parts.

The nutrient content as mg/m² of leaves showed significantly more of most nutrients in the large producing plants except for manganese, silicon, sodium and zinc, which were similar for both large and small plants, regardless of fruit production. New stems appear to function mainly as transport organs, with few significant differences in the nutrient content per meter square. Old stems are major nutrient sinks with significantly more of all nutrients except manganese and zinc in the large producing plants than in the large or small non-producing plants. Rhizomes held less total nutrient per meter square than the old stems or leaves, but more than the new stems. Rhizomes tended to have significantly more nutrient in the large producing plants per meter square, compared to the large and small non-producing plants. Fine roots proved to be nutrient sinks also, storing considerable amounts of nutrients per gram, but constituting an extremely small biomass on an area basis. Thus, plants that are able to produce good fruit crops are generally larger (\bar{X} of 2,441 g dry weight/m² compared to non-producing plants, 790 to 1,986g/m²) and have the largest total nutrient storage in nearly all compartments except the new stems.

This raises the question of how the high producing plants are able to accumulate so much more nutrients and biomass. One hypothesis is that lack of water stress would allow better nutrient uptake and availability and might result in better mycorrhizal formation.

It is also valuable to look at the concentration of nutrients in the individual plant parts as micrograms per gram expressed as per gram of total plant weight. This method of expression removes the problem of differences in the relative weight of the various plant parts. When data were expressed in this manner, leaves of the large producing and large and small non-producing plants showed little significant differences in nutrient concentration. This means that it takes so much nutrient to produce a gram of leaf, regardless of

how many leaves there are per meter square. Only boron and copper showed significantly higher concentrations in the high producing plants, suggesting that these should be tested as possibly limiting factors to production. Differences in the amount of total copper remained important per gram of total plant for the old stems of the high producing plants. Thus, old stems function as reservoirs for nutrients and are a good tissue to examine for possible nutrient deficiencies. Rhizomes had surprisingly high concentrations of iron, phosphorus and aluminum in the young non-producing plants, suggesting that these nutrients are important to young growing plants.

Data of this type ($\mu\text{g/g}$ of plant) from the whole plant are useful when formulating fertilizer that will meet the growth demands of plants in different stages of development and for possibly stimulating non-producing large plants to produce. On the basis of whole plants, the large producing plants had the most aluminum, boron, calcium, copper, potassium and phosphorus, while small non-producing plants had the most iron and sodium. Large non-producing plants had significantly low levels of aluminum, copper, iron, potassium, sodium and phosphorus. This suggests that fertilizers that would supplement these available soil nutrients may, in the absence of other stresses, stimulate fruit production. This hypothesis will be tested in the near future. Although sodium is not known to be an essential nutrient to growth of these plants, it is thought to be important in maintaining osmotic potentials needed to bring in water that is essential to cell expansion.

Certain plant parts act as sinks for different nutrients. Nitrogen, boron, magnesium and silica were stored in large amounts in the flowers and leaves, while roots stored aluminum and iron. Roots stored the most copper and iron. Significant amounts of potassium occurred in the flowers, and old stems stored considerable copper and zinc. Work by Ingstad (1973) showed that *V. vitis-idaea* and *V. myrtilloides* had low potassium requirements and rapid calcium uptake, compared to other woody species of forest plants. Both nitrate and ammonium forms were used by these species of *Vaccinium*.

Xylem Sap Analysis

The field technology for the extraction and analysis of xylem sap from trees has been adapted to shrubs as a means of evaluating the nutrient status of shrubs (Stark and others 1985). The main modification for shrubs is that the tygon tubing that is attached to the cut end of the branch that extends outside of the pressure chamber is fastened to a small vial and the sap is allowed to flow from the branch directly into the vial.

Results of xylem sap analysis from high production plants showed significantly higher levels of boron, iron, magnesium, sodium and nitrogen than xylem sap from plants in areas that rarely produce fruit. Climatic factors and nutritional factors are thought to interact to make a particular site conducive to high fruit production.

ORGANIC COMPOSITION

Large producing plants had significantly more total nitrogen, total non-structural carbohydrates, caloric content and ash content on a meter square basis. Large non-producing plants had more cellulose, but nearly the same amounts of tannin and lignin as the large producing whole plants. Small non-producing plants had a third of the total nitrogen that occurred in the large producing plants, and about a third of the total nitrogen. On a concentration basis, large producing plants had 17,027 ppm nitrogen while small non-producing plants had 14,340 ppm in the foliage.

The lignin content of the old stems and rhizomes was high compared to other plant components. The tannin content of the leaves was higher than that in other plant parts. The tannin content of foliage does not appear to be an effective deterrent to herbivory because the leaves are readily eaten by several insects and other higher animals. Tent caterpillars eat the foliage readily.

SOILS

Soils from sites with high fruit production had significantly higher concentrations of boron, calcium, magnesium, phosphorus, zinc, and total nitrogen than soils from non-producing sites. This trend for higher soil organic matter and available nutrients has been found consistently on sites with high fruit production, prompting the conclusion that good fruit production is most likely to occur on the more fertile soils and those with more organic matter and available soil moisture.

The results of these and other studies have provided considerable assistance in the development of a commercial huckleberry growth strategy.

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COMPARATIVE GROWTH OF FOUR SHRUB SPECIES IN A NATIVE DESERT SOIL AND

AN AMENDED NON-CALCAREOUS SOIL AND SOME UNSOLVED PROBLEMS IN

MINERAL NUTRITION OF DESERT SHRUBS

Arthur Wallace

ABSTRACT: Four desert shrub species native to the northern Mojave Desert were grown in a non-saline but calcareous soil from that desert and in a non-calcareous non-saline soil for four months with and without gypsum and lime amendments. The species were Larrea tridentata, Ambrosia dumosa, Ceratoides lanata, and Grayia spinosa. Growth for three species was higher in the non-calcareous soil than in the desert soil which is from an area where all four species grow naturally. The one species that did not grow better in the non-calcareous soil was one that is a high accumulator of K. All four species responded positively to Ca and Mg sulfates applied to the non-calcareous soil. Calcium and Mg carbonates applied to the non-calcareous soil depressed growth of L. tridentata, while only Mg carbonate decreased that of A. dumosa and C. lanata. Both carbonates improved growth of G. spinosa, although the increases were not different at the 0.05 level of significance. Adaptation of these four species to desert conditions may be due largely to factors other than soil characteristics. Among the unsolved nutritional problems of desert shrubs are those related to differential accumulation and partitioning of cations, especially Na, for different species that grow side by side at the same locations. Cation-anion ratios in these plants are of considerable interest in relationship to micronutrients.

INTRODUCTION

Most desert-plant species grow in soil which is highly calcareous and often in soil which is also high in gypsum. The purpose of this study was to determine if four representative species from the northern Mojave Desert are obligate for CaCO_3 , MgCO_3 , or gypsum. The purpose was not to explain the mineral relationships of the desert plants used, although the study contributes to that also. Mineral composition of these species has been reported (Romney and others 1973; Wallace and others

1972). The comparative mineral nutrition of native plants is a subject about which more information would be useful, especially for desert shrubs (Gerloff 1963). Species with greatly differing nutrient requirements often grow side by side.

MATERIALS AND METHODS

Single Larrea tridentata (Ses. and Moc.) seedlings, Ambrosia dumosa (Gray) seedlings, Ceratoides lanata (Pursh) Moq. cuttings, and Grayia spinosa (Hook.) Moq. cuttings were grown in pots of soil in a glasshouse. The G. spinosa plants were chilled at 5C one week before beginning the test so that their growth would be normal (Wallace and others 1970). Soil used was either nearly neutral Yolo loam (a Xerorthents from California) or a highly calcareous soil (a Durargid from Mercury, Nevada). The Yolo loam was amended to give various treatments: 2% CaCO_3 , $\frac{1}{2}\%$ MgCO_3 , $\frac{1}{2}\%$ CaSO_4 , $\frac{1}{2}\%$ MgSO_4 , 2% CaCO_3 + $\frac{1}{2}\%$ MgCO_3 , 2% CaCO_3 + $\frac{1}{2}\%$ MgCO_3 + $\frac{1}{2}\%$ CaSO_4 , 2% CaCO_3 + $\frac{1}{2}\%$ MgCO_3 + $\frac{1}{2}\%$ CaSO_4 + $\frac{1}{2}\%$ MgSO_4 . Plants were grown in 1000-g quantities of these soils for four months (January through April). The glasshouse temperature ranged from 22 to 28C daytime and 15 to 20C night. Nitrogen was applied five times during the test, and sufficient N as NH_4NO_3 was added each time to give 15 mg N kg^{-1} soil. Once each week a solution of 10^{-3}M KH_2PO_4 was used as an irrigating solution. The plants were irrigated otherwise with distilled-deionized water as needed to maintain soil moisture near -0.03 MPa. Pots had bottom drain holes so the CaSO_4 in various treatments was renewed during the test. Each treatment was in triplicate. At the end of the four months the shoots were cut 1 cm above the soil line and washed with 1/10 N HCl and then with distilled-deionized water. Dry weights were determined, and plants were prepared for mineral analyses by optical emission spectrometry (Alexander and McAnulty 1981).

RESULTS AND DISCUSSION

When grown in the Yolo loam soil, L. tridentata responded positively to CaSO_4 and slightly negatively to the CaCO_3 and MgCO_3 (table 1). Plants with MgCO_3 tended to be slightly chlorophyll deficient; but Zn, Cu, Fe, and Mn levels did not seem to be decreased. Molybdenum was increased by some liming materials as is well known (Evans and others 1951). Magnesium levels were increased by the Mg-containing materials. MgCO_3 alone decreased the P

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contents of plants. *L. tridentata* plants grown in the desert soil were much smaller than those grown in the Yolo loam soil, particularly when carbonates had not been added to the Yolo soil.

All *A. dumosa* grown in $MgCO_3$ had chlorophyll-deficient leaves in varying degrees and yields (table 1) were related to this phenomenon. Growth was increased slightly by Ca-containing amendments, but not significantly in the test. Magnesium concentrations were increased by Mg amendments. Phosphorus concentrations were decreased with liming materials; $MgCO_3$ caused greater decreases than did $CaCO_3$. Zinc and Mn concentrations of these plants were decreased by the liming materials, but liming had no effect on Fe concentrations.

Highest yields of *C. lanata* were with $CaSO_4$ (table 1). Yields with $MgCO_3$ were generally decreased, but the leaves showed no chlorophyll deficiency. The Mg materials increased the Mg concentrations of leaves and simultaneously decreased those of Ca. Mg had more effect than Ca on Ca concentrations of leaves, but the Mg effect was negative. Liming materials decreased P concentrations of leaves. They also decreased Zn, Cu, and Mn in this species, but not Fe concentrations of leaves. Yields of *C. lanata* grown in the desert soil were like those of the control Yolo soil in contrast to *L. tridentata* and *A. dumosa*.

G. spinosa responded favorably to $CaSO_4$, but not to $CaCO_3$ or $MgSO_4$ (table 1). The latter two, however,

Table 1--Yields of shoots and mineral composition of leaves of plants grown with various lime materials in Yolo loam soil

Treatment ¹	<i>L. tri- dentata</i>	<i>A. dumosa</i>	<i>C. lanata</i>	<i>G. spinosa</i>	<i>L. tri- dentata</i>	<i>A. dumosa</i>	<i>C. lanata</i>	<i>G. spinosa</i>	<i>L. tri- dentata</i>	<i>A. dumosa</i>	<i>C. lanata</i>	<i>G. spinosa</i>
dry weight yield					Ca				Mg			
	mg plant ⁻¹				% of dry weight				% of dry weight			
Control	549	814	1033	436	1.35	1.99	1.13	0.48	0.24	0.44	0.40	0.69
2% $CaCO_3$	284	960	940	568	1.32	1.97	1.04	0.77	0.25	0.39	0.35	0.75
1/2% $MgCO_3$	240	427	644	546	1.26	1.21	0.93	0.65	0.48	0.69	0.56	1.33
1/2% $CaSO_4$	919	1118	1426	887	1.48	1.95	1.21	0.92	0.22	0.33	0.41	0.79
1/2% $MgSO_4$	482	1152	1245	761	1.19	1.40	0.86	0.59	0.41	0.64	0.58	0.85
$CaCO_3$ + $MgCO_3$	398	429	765	369	1.11	1.15	1.02	0.65	0.45	0.63	0.58	1.18
$CaCO_3$ + $MgCO_3$ + $CaSO_4$	303	397	824	652	1.59	1.45	1.11	0.58	0.42	0.64	0.55	1.10
$CaCO_3$ + $MgCO_3$ + $CaSO_4$ + $MgSO_4$	358	370	1295	800	1.23	1.20	0.92	0.58	0.49	0.80	0.69	1.09
Nevada desert soil	133	368	952	463	1.53	2.51	1.47	1.36	0.35	0.59	0.49	0.74
LSD 0.05	253	352	510	370	0.25	0.47	0.20	0.55	0.09	0.12	0.08	0.25
P					Zn				Cu			
	% of dry weight				mg kg ⁻¹				mg kg ⁻¹			
Control	0.39	0.57	0.96	2.64	39	71	52	109	6	7.6	10.0	35
2% $CaCO_3$	0.32	0.45	0.35	1.07	32	40	38	38	8	6.0	7.8	19
1/2% $MgCO_3$	0.26	0.35	0.31	0.77	34	45	36	50	7	8.0	8.3	25
1/2% $CaSO_4$	0.37	0.62	0.93	2.37	51	68	53	107	7	7.6	11.7	44
1/2% $MgSO_4$	0.38	0.54	1.10	2.11	47	62	66	88	6	7.0	12.0	35
$CaCO_3$ + $MgCO_3$	0.30	0.46	0.35	0.81	42	30	37	43	10	8.7	8.6	19
$CaCO_3$ + $MgCO_3$ + $CaSO_4$	0.44	0.32	0.32	0.51	48	39	37	43	10	9.0	7.3	16
$CaCO_3$ + $MgCO_3$ + $CaSO_4$ + $MgSO_4$	0.37	0.20	0.39	0.52	38	44	34	48	16	8.2	7.7	16
Nevada desert soil	0.25	0.17	0.26	0.30	51	65	38	46	3	1.7	1.8	3
LSD 0.05	0.07	0.06	0.12	0.41	11	11	16	25	5	3.6	1.7	10
Fe					Mn				Mo			
	mg kg ⁻¹				mg kg ⁻¹				mg kg ⁻¹			
Control	124	63	46	38	28	180	85	85	1.4	1.0	1.3	10.6
2% $CaCO_3$	95	61	39	30	26	55	43	47	8.1	3.7	3.5	12.0
1/2% $MgCO_3$	186	77	49	40	37	87	47	108	7.0	2.3	2.0	11.3
1/2% $CaSO_4$	124	61	45	35	23	160	102	172	0.8	0.8	0.6	3.7
1/2% $MgSO_4$	194	60	55	53	22	166	176	94	0.9	1.2	0.6	3.3
$CaCO_3$ + $MgCO_3$	101	63	48	44	28	57	33	51	5.0	1.3	2.6	8.5
$CaCO_3$ + $MgCO_3$ + $CaSO_4$	107	81	44	27	37	81	48	57	1.0	0.5	0.5	4.3
$CaCO_3$ + $MgCO_3$ + $CaSO_4$ + $MgSO_4$	113	68	50	33	72	79	49	78	0.9	0.9	0.7	3.8
Nevada desert soil	272	81	45	28	29	44	17	9	0.7	0.9	0.5	1.8
LSD 0.05	57	ns	ns	ns	20	35	42	37	2.5	0.9	1.1	2.6

¹Concentrations of each amendment was similar in the combinations to those for single applications.

did not decrease growth. Calcium and Mg treatments increased Ca and Mg in leaves, respectively; but there was no evidence of an inverse relationship between the two elements in contrast to some of the other plants. Phosphorus levels were high in leaves, but were decreased by liming materials. Zinc and Ca were decreased by the liming materials. The Cu content of *G. spinosa* leaves was considerably higher than of the other two species. Manganese was decreased by CaCO_3 , but not by MgCO_3 . Again, the yields were not decreased for the plants growing in the desert soil.

None of the four plant species seemed to have a lime requirement, even though they normally grow in calcareous soil. All four of the species seemed to respond to CaSO_4 (gypsum), but only two were statistically significant. More study is needed to determine if gypsum at a given level is an absolute requirement of these species or if they have a high requirement for S.

SOME UNSOLVED PROBLEMS IN MINERAL NUTRITION OF DESERT PLANTS

In addition to the problems discussed above concerning the obligate nature of desert shrubs for specific soil types, such as high lime, gypsum, saline or sodic or others, there are other questions of interest for which answers have not been obtained. Among these are those related to large differences in cation accumulation for species growing in close proximity to each other (table 2). *G. spinosa* is an accumulator of K, and it grows close to *Lycium andersonii*, which is a marked

accumulator of Ca. *Mirabilis pudica* strongly accumulates Mg compared with other species with which it is associated. *Atriplex confertifolia* accumulates considerable Na while growing close to species which do not. At site 22, plant leaves accumulated little Na, and 58% of the cation sum in *G. spinosa* was K, while it was only 5% in *M. pudica*. The cation sum varied considerably among species. One species of *Lycium* accumulated considerable Na in leaves, while another did not. *Acamptopappus shockleyi* ordinarily grows in bare soil between shrub clumps where N is poorly available. The leaf analysis consistently indicates lower N and higher Si concentrations than for some species growing in clumps. In fact, the Si in this species approaches that for the grass species *Oryzopsis hymenoides* shown in table 2.

Many possible research projects are indicated in these sample data. Chloride analyses were not obtained for these samples and would, with P, give a more complete picture for anions. Some of the problems have been studied in part. In one study, three of the species were grown in solution culture with and without Cl, and cation-anion ratios were determined (Wallace and others 1974). With *A. confertifolia* and *A. hymenlytra* in the whole plant, cation uptake greatly exceeded anion uptake which implies that protons are excreted to the soil and that the plants would contain higher levels of organic acids. This characteristic is indicative of Fe efficiency (Romheld and Marschner 1984; Wallace and others 1968). (See Nelson and Jolley, these proceedings.) In *L. andersonii*, Ca was less available than for soil, and from some of the solutions anion uptake equaled or exceeded cation

Table 2--Cation and some anion concentrations in leaves. Some shrub and other plant species growing in close proximity to each other at the Nevada Test Site (Adapted from Romney and others 1973)

Species	Na	K	Ca	Mg	Cation sum	N	Si
me 100 g ⁻¹ dry weight							
from site 22							
<i>Ceratoides lanata</i>	1	83	134	43	261	254	10
<i>Grayia spinosa</i>	7	302	89	121	519	234	5
<i>Larrea tridentata</i>	1	68	113	16	197	222	14
<i>Lycium andersonii</i>	1	86	458	75	620	290	7
<i>Mirabilis pudica</i>	0	26	248	198	504	212	11
<i>Oryzopsis hymenoides</i>	1	80	41	24	145	171	119
from site 51							
<i>Atriplex confertifolia</i>	167	188	216	66	637	96	10
<i>Grayia spinosa</i>	72	204	115	97	488	155	3
<i>Larrea tridentata</i>	1	62	65	15	143	163	9
<i>Lycium andersonii</i>	7	105	482	81	675	179	7
<i>Lycium pallidum</i>	47	81	206	147	481	126	10
one species from two different sites							
<i>Acamptopappus shockleyi</i>	6	106	87	52	251	186	64
<i>Acamptopappus shockleyi</i>	8	98	63	66	235	166	55

uptake. This implies that the biochemistry of roots may need to split H_2O to yield H^+ and OH^- with the latter metabolized (Wallace and Wallace 1984) for Fe to become available, but this has never been proved as yet.

Another species of *Atriplex* (*canescens*) accumulates Na in roots, but translocates very little to shoots (Wallace and others 1973b). The mechanisms for such partitioning have not been elucidated. The three species of *Lycium* found at the Nevada test site differ greatly in their responses to Na, and one (*L. shockleyi*) grows only in some saline habitats (Ashcroft and Wallace 1976). When grown in solution culture, cation ratios exceeded anion ratios for all species, although only moderately. Studies of proton release, Fe uptake, organic acid metabolism, and other characteristics are indicated for all these species. *Artemisa tridentata* appears to be a species in which anion uptake exceeds cation uptake (Wallace and others 1973a) and would be a subject of interesting studies, especially for Fe relations.

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 PHYSIOLOGICAL CHANGES IN CHRYSOTHAMNUS NAUSEOSUS IN RELATION TO RUBBER AND RESIN PRODUCTION //

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ABSTRACT: Of particular interest in Chrysothamnus nauseosus (rubber rabbitbrush) is the presence of natural rubber that has potential commercial value. The factors that regulate rubber or resin production are of special interest because of the potential of increasing the rubber content. Rubber rabbitbrush, maintained under irrigation, exhibits relatively high rates of net photosynthesis for a woody species throughout the growing season. Net photosynthesis is generally highest during cool morning hours (0900-1000 h) and is not light saturated at light levels equivalent to full sun. The changes in rubber and resin content in new growth, one-year-old tissue, and several-years-old tissue were followed during the growing season in Chrysothamnus nauseosus ssp. turbinatus and Chrysothamnus nauseosus ssp. hololeucus. The top of the plants contained the highest level of resin and the lowest amount of rubber. In contrast, the highest rubber content and lowest resin content were in the older stems near the soil level. The negative correlation between the rubber and resin was high ($r^2 = 0.64$, $p = 0.03$). When the rubber and resin contents were followed through the growing season, the highest rubber content and lowest resin content occurred during August. In contrast, the highest resin and lowest rubber occurred in the spring. The negative correlation between rubber and resin in one-year-old stems of ssp. turbinatus was high ($r^2 = 0.76$, $p = 0.004$). A bioregulator treatment (paclobutrazol) significantly ($p < .05$) increased resin content and decreased rubber content.

INTRODUCTION

Chrysothamnus nauseosus (rubber rabbitbrush) is widely distributed in the western United States (Anderson 1986). Subspecies of C. nauseosus occur from Mexico to Canada, from sea level to 3,000 m above sea level and on disturbed sites

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and saline soils (McArthur and others 1979; McArthur 1984). Rubber rabbitbrush is a diversified species that survives well under conditions that cause considerable stress to most plants. It is of particular interest that rubber rabbitbrush contains natural rubber that may have commercial value (Hall and Goodspeed 1919; Weber and others 1985; Ostler and others 1986). The factors that regulate the production of rubber in rabbitbrush are not well understood. This paper reviews progress we have made in that area and presents new data on physiological response to stress conditions.

PHOTOSYNTHETIC CHARACTERISTICS

Rubber rabbitbrush fixes carbon dioxide by the C_3 pathway as indicated by its C_{13}/C_{14} ratios (Smith 1987). Yet this plant exhibits relatively high rates of net photosynthesis (Pn) as compared to other woody C_3 plants. On both leaf area and dry weight bases, the rate of Pn of C. nauseosus ssp. albicaulis is similar to the C_4 desert shrub Atriplex canescens. The carbon dioxide fixing enzyme, RuBP carboxylase, and intercellular CO_2 contents of rubber rabbitbrush are similar to those found in most C_3 crop species (Davis and others 1985). An interesting ecophysiological aspect of rubber rabbitbrush Pn is that photosynthesis is not light saturated at light levels that are equivalent to full sun, perhaps due to the presence of leaf pubescence. This may be a useful, adaptive characteristic for a plant that exists in a desert environment with high light intensity. It has been reported that pubescence on leaves of desert plants reduces the light absorbance resulting in reduced heart loads and lower leaf temperatures (Ehleringer and Bjorkman 1978; Ehleringer and Mooney 1978). Rubber rabbitbrush is capable of maintaining high Pn and high stomatal conductance under well-watered conditions, which results in high rates of dry matter accumulation per unit of biomass (Davis and others 1985; Davis 1987). Rates of rubber rabbitbrush Pn are generally highest during cool morning hours (between about 0900 and 1000 hrs). Pn declines considerably during mid-day hours on hot summer days, probably due to partial stomatal closure (Davis 1987). Biomass studies by McKell and Van Epps (1980) reported that individual rubber rabbitbrush plants that had been clipped and allowed to grow for 2 years yielded average values of 5,670 g per year. Hall and Goodspeed (1919) reported an average growth rate for rubber rabbitbrush of 3,345 to 3,799 g per year in natural populations.

RUBBER AND RESIN CONTENT

Rubber and resin contents of *Chrysanthamnus* were first surveyed by Hall and Goodspeed in 1919. They reported an average rubber content of 1.7% from 140 different samples. They found two subspecies that had a rubber content of 6% (Hall and Goodspeed 1919). In 1982, Ostler and others (1986) made a number of new collections of rabbitbrush and found populations with 6.5% rubber. In 1984, Hegerhorst and others (1987c) made a number of collections from natural populations of rubber rabbitbrush and found that *C. nauseosus* ssp. *turbinatus* populations contained 7% rubber.

The resin content of rubber rabbitbrush is of significance because of its potential value as a hydrocarbon source, as potential insecticides, fungicides, and nematocides, and as a chemical feedstock for chemical companies. Buchannon and others (1978) evaluated over 100 plant species as potential hydrocarbon crops and both rubber rabbitbrush and its composite family relative,

guayule, rated high. Rubber rabbitbrush had a slightly higher hydrocarbon rating with a value of 11.5%. Natural insecticides from rubber rabbitbrush have been reported by Bohlmann and others (1979a, 1979b), Rose and Jermy (1980), and Maugh (1982), and may have some commercial value.

THE GROWING SEASON STUDY

In 1919 Hall and Goodspeed reported that rubber in rubber rabbitbrush was located in older wood. Hegerhorst and others (1987c) recently analyzed the rubber and resin content from the top to the bottom of individual plants of *C. nauseosus* ssp. *turbinatus* (Jones) Hall & Clem (high rubber content about 5-7%) and ssp. *hololeucus* (Gray) Hall & Clem (low rubber content about 1.5%). The rubber and resin were determined by the method of Hegerhorst and others (1987c). They found that the highest resin content and the lowest rubber content were in the leaves and new shoots of the plant (fig. 1). In contrast, the highest rubber content was in the older stems near the soil

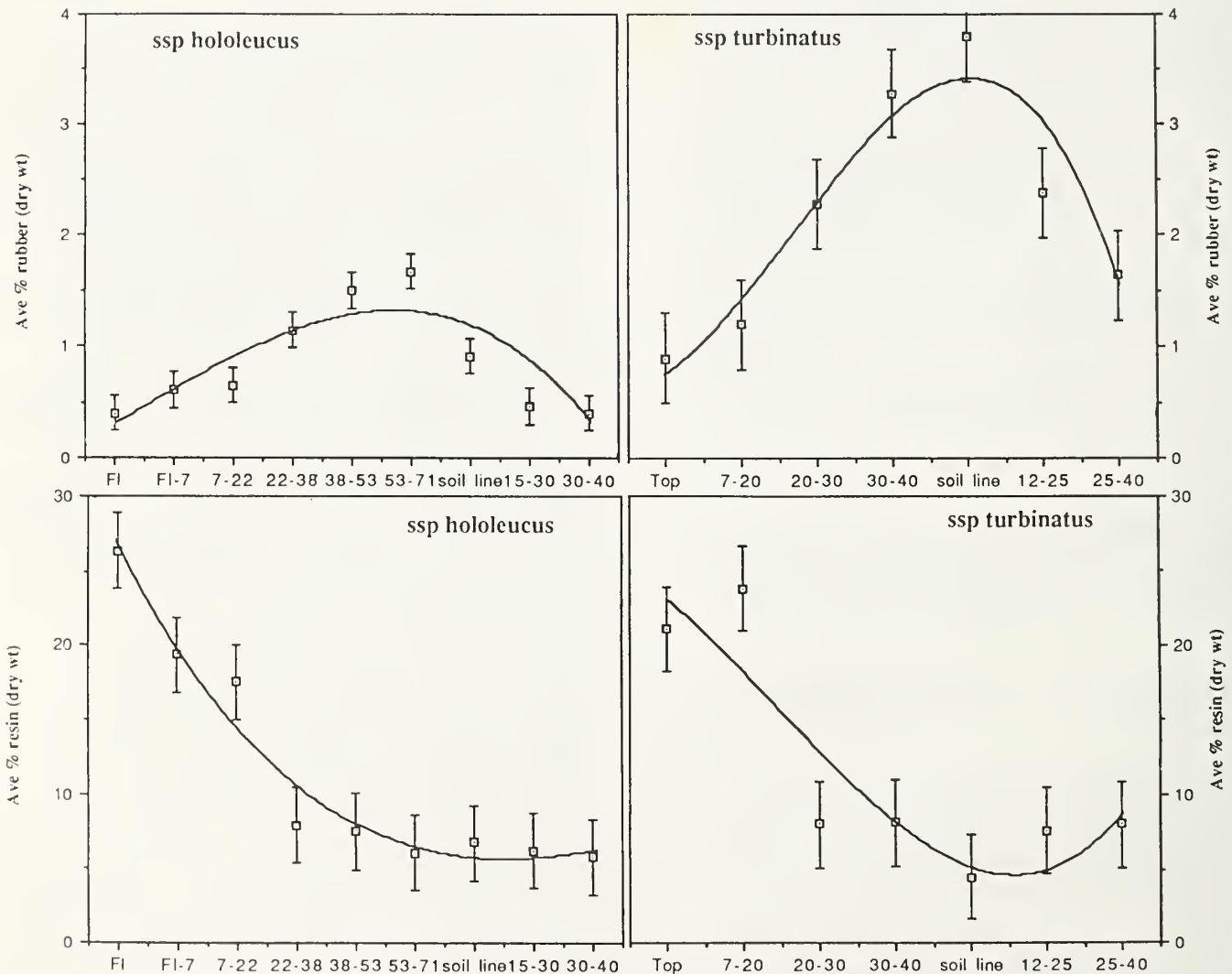


Figure 1--Average percent resin and rubber from top to bottom of *C. nauseosus* ssp. *turbinatus* (right) and *C. nauseosus* ssp. *hololeucus* (left). Vertical lines represent standard error bars (Hegerhorst and others 1987b).

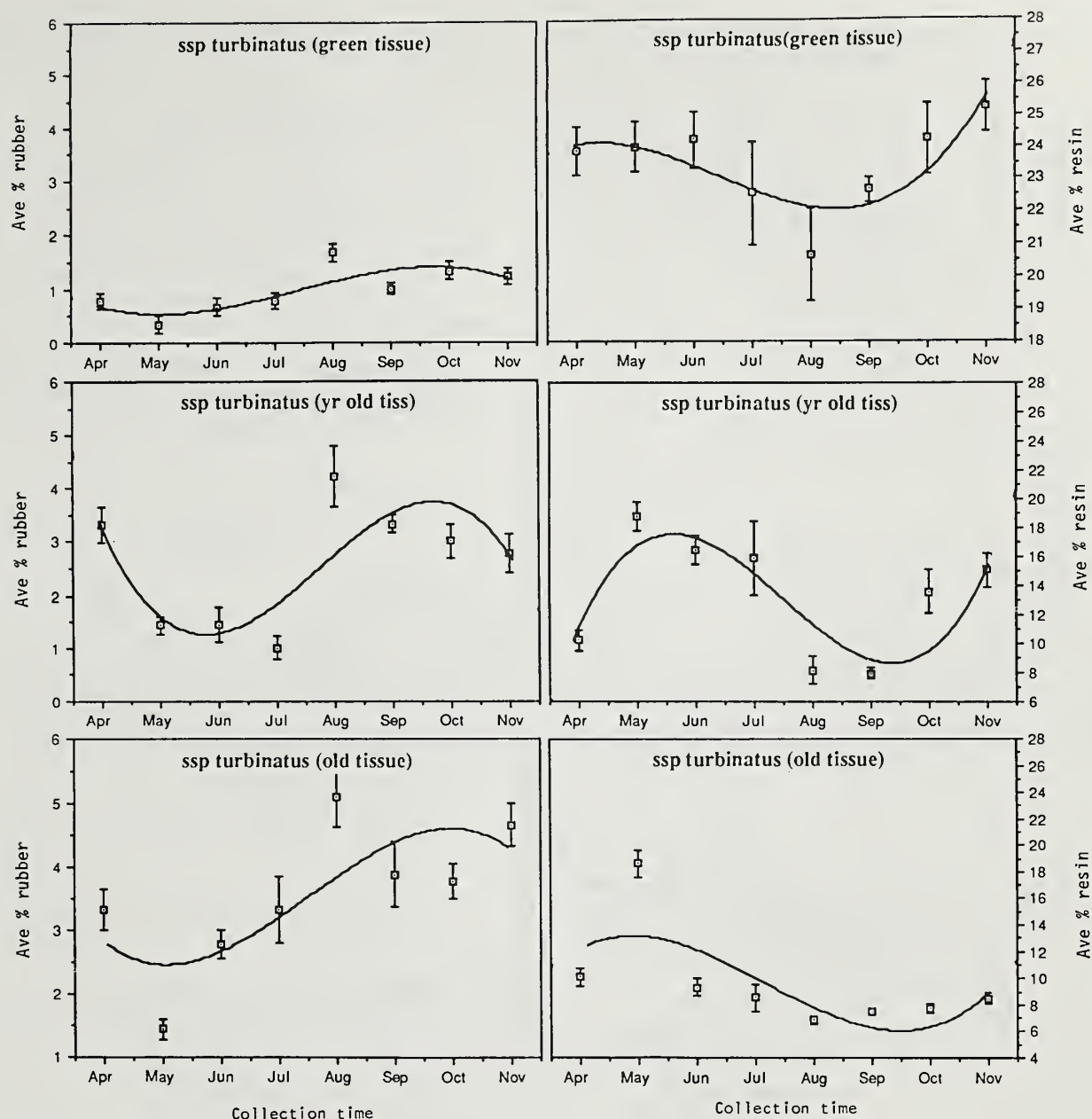


Figure 2--The average percent rubber and average percent resin in green tissue, year-old tissue, and several-years-old tissue of *C. nauseosus* ssp. *turbinatus* during the growing season at Goshen, Utah. Vertical lines represent standard error bars (Hegerhorst and others 1987b).

level. The rubber content was also fairly high in the upper roots but dropped off rapidly with increasing depth in the soil (fig. 1). The negative correlation between rubber and resin was strong ($r^2 = 0.64$, $p = 0.03$).

Changes During the Growing Season

Tissue samples of new growth, one-year-old growth, and several-year-old growth were taken monthly from the two sympatric subspecies *turbinatus* and

hololeucus growing near Goshen, Utah. The tissue was ground with a motorized steel mortar and pestle, using liquid nitrogen to freeze the tissue. After grinding, the tissue was stored in a freezer until analyses. The ground tissue was extracted for rubber and resin using the method of Hegerhorst and others (1987c).

The highest content of rubber and lowest resin content in *turbinatus* occurred in August, whereas the highest resin and lowest rubber content occurred in the spring (fig. 2). In contrast,

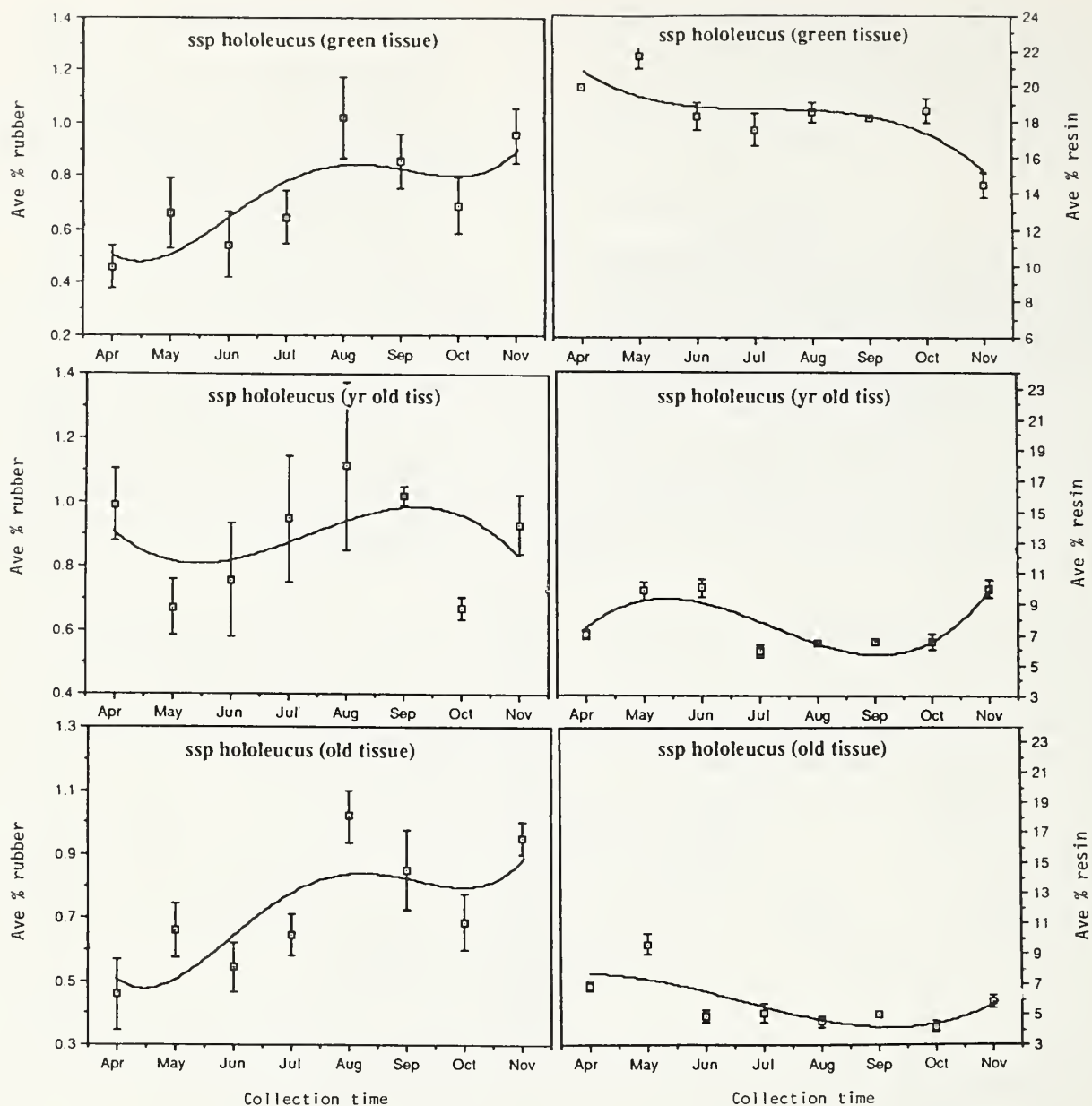


Figure 3--The average percent rubber and average percent resin in green tissue, year-old tissue and several-years-old tissue of *C. nauseosus* ssp. *hololeucus* during the growing season at Goshen, Utah. Vertical lines represent standard error bars (Hegerhorst and others 1987b).

guayule has the highest rubber content in the winter (Foster and others 1983; Bucks and others 1986). The negative correlation between rubber and resin was very high ($r^2 = 0.76$, $p = 0.004$). A similar rubber and resin pattern was present in *ssp. hololeucus* (fig.3) except the negative correlation was not as high. Also rubber content was considerably lower in *ssp. hololeucus* as compared to *ssp. turbinatus*.

The summer months of June, July, and August are periods of high temperature and low rainfall for the Goshen site (fig. 4) (Stevens and others 1983). This presumably would be a period of high water stress for plants growing on the site. Ostler and others (1986) have analyzed the environmental conditions at different collection sites of rubber rabbitbrush and concluded that stressful conditions were correlated with higher rubber content. The results of Hegerhorst and others (1978b) also suggest a strong correlation between stress and rubber content. It is not clear at this time whether rubber is a type of osmotic protectant against heat and water stress, but peak rubber content is correlated with the period when plants presumably experience high stress. This observation suggests that rubber and resin production is dynamic and can perhaps be regulated by environmental factors.

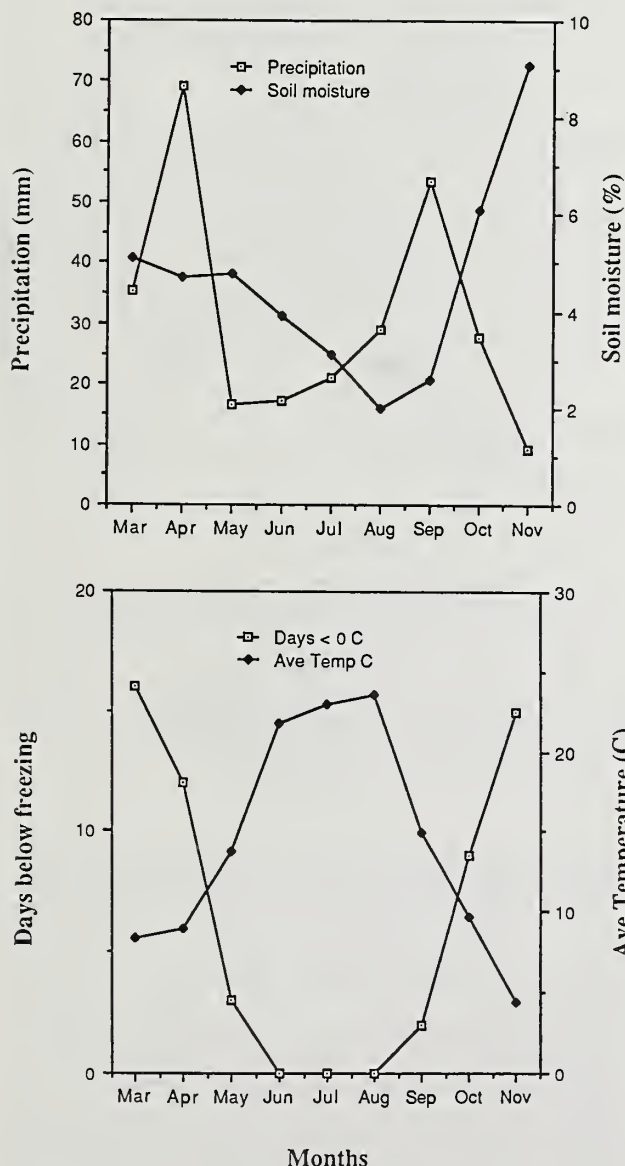


Figure 4--(upper) Precipitation (mm) and soil moisture (percent) and (lower) average temperature and days below freezing during the growing season at Goshen, Utah (Hegerhorst and others 1987b).

The change in the rubber and resin content in rabbitbrush could be explained in a number of ways. One possibility is that the resin production enzymes are more heat sensitive and are inactivated at higher temperatures. In contrast, the rubber production enzymes may be more temperature stable and able to continue to function during periods of stress similar to the heat shock protein of soybeans (Key and others 1985). Another possible explanation for rubber and resin changes could be that the same basic pathway is functioning in both cases but the pathway has a junction point where the compounds are directed to resin production or rubber production. The partitioning of metabolites between the two pathways may be regulated by stress. Thus under periods of high stress the activity of the rubber pathway would be increased, whereas under periods of low stress the resin production would be favored. Further investigations are necessary to test these two hypotheses.

Another question which arises from these results is whether resin is broken down and converted to rubber and vice versa. The inversely correlated changes in the rubber and resin content would suggest that catabolic enzymes are functioning. This resin-rubber relationship would be an important aspect in storing harvested plants or in trying to stabilize rubber content before harvesting. Labeling experiments should be able to indicate whether breakdown and synthesis of the smaller compounds into rubber occur.

Changes in Other Secondary Metabolites

The contents of secondary metabolites in the resin extract were determined by GC-MS over the growing season. The total compounds in the cyclohexane fraction (fig. 5) followed the general resin

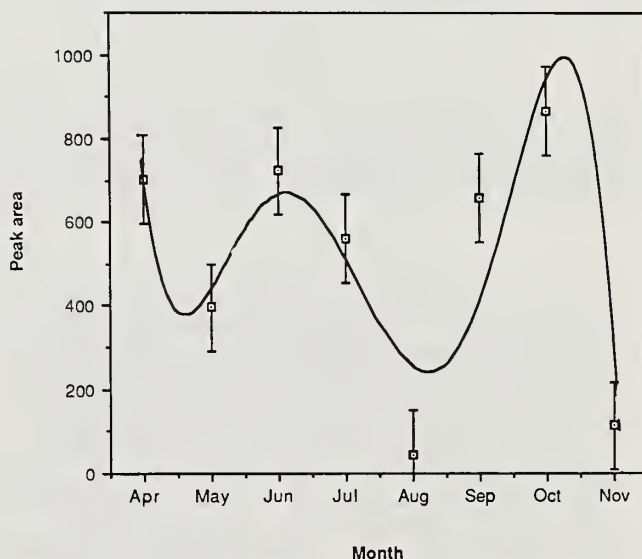


Figure 5--Total compounds in the cyclohexane fraction from *Chrysothamnus nauseosus* ssp. *turbinatus* during the growing season at Goshen, Utah. Vertical lines represent standard error bars (Hegerhorst and others 1987a).

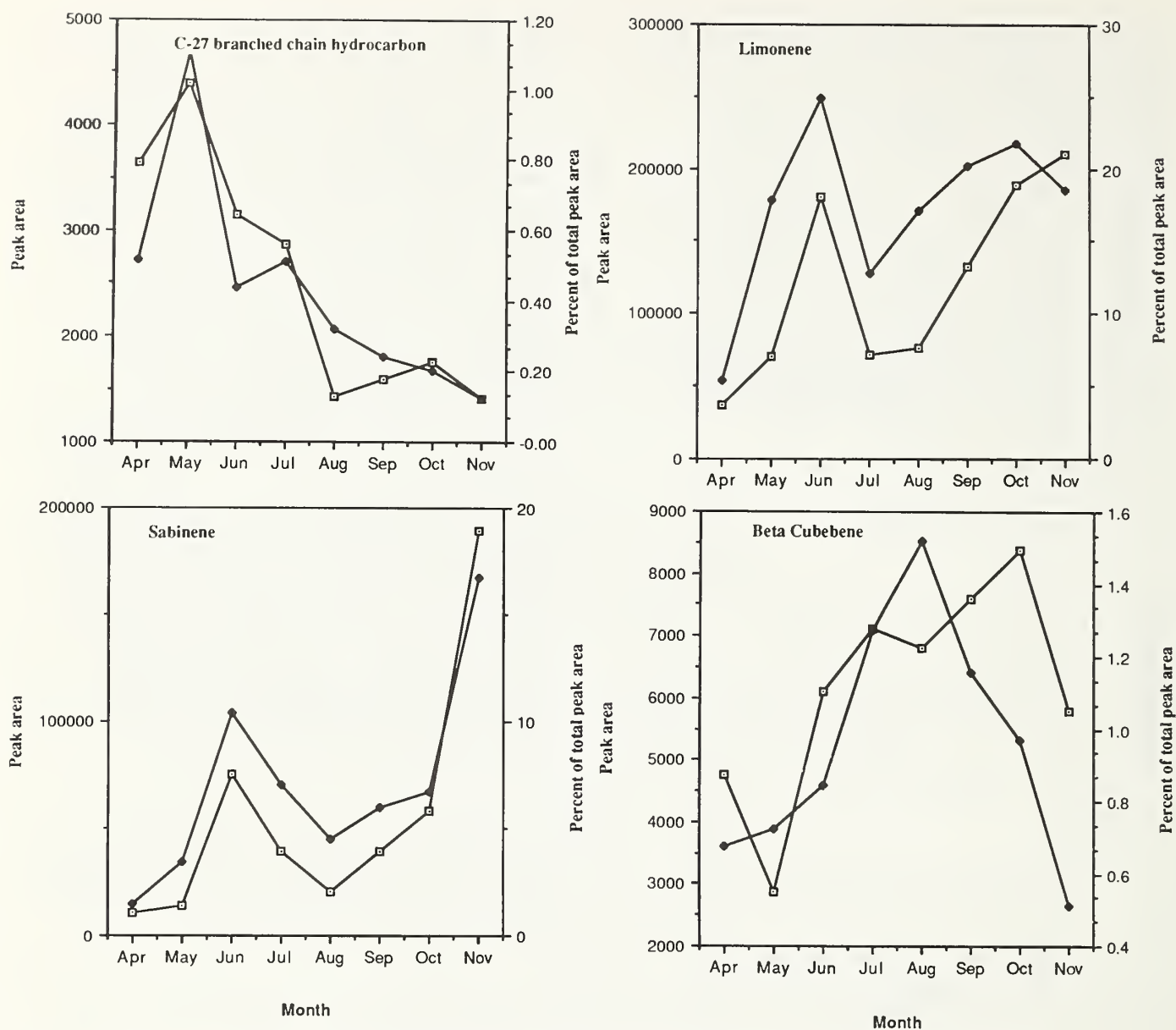


Figure 6--Changes in C-27 branched hydrocarbon (top left), Limonene (top right), Beta Cubebene (bottom right), and Sabinene (bottom right) from *Chrysothamnus nauseosus* ssp. *turbinatus* during the growing season at Goshen, Utah. The square represents the percent of the area of the compound in relation to the total area of all the compounds (Hegerhorst and others 1987c).

pattern but individual compounds varied within the growing season (Hegerhorst and others 1987a, 1987d). Simple and branched chain hydrocarbons increased in the early spring and then decreased throughout the remainder of the growing season (fig. 6). Limonene content was negatively correlated with rubber content but positively correlated with resin content (fig. 6). On the other hand Cubebene was positively correlated with rubber content and negatively correlated with resin content (fig. 6). A few compounds did not follow either pattern, such as Sabinene, which was low in the spring and increased during the growing season (fig. 6). Further studies are needed to elucidate the metabolite relationship

between the changes in these compounds and changes in rubber and resin content.

DISTRIBUTION ALONG A STRESS GRADIENT

Samples of *Chrysothamnus* ssp. *hololeucus* were collected from the alluvial fan at the base of a steep slope and up the slope along a water stress gradient (Freeman and others 1987) in Kingston Canyon, south of Richfield, Utah. In addition to the water stress gradient established by Freeman and others (1987), we looked at several other soil factors that might influence plant physiological processes. Soils from the

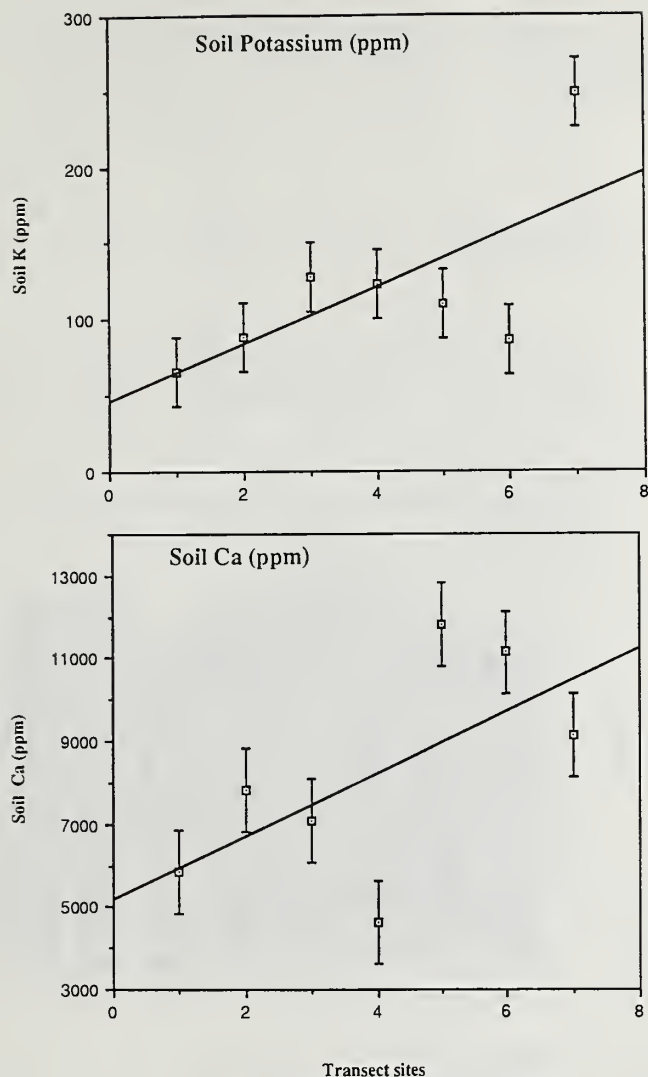


Figure 7--The potassium concentration (ppm) and the calcium concentration (ppm) in the soil from seven sites along a water stress gradient in Kingston Canyon south of Richfield, Utah. The lines were drawn by the method of least squares. Vertical lines represent standard error bars.

different collection sites on the alluvial fan and up the slope were collected and analyzed for percent silt, percent sand, percent clay, pH, P, NO_3 , K, Ca, and Mg at the Brigham Young University soil laboratory using methods outlined by Hesse (1971). Potassium and Ca increased in concentration up the slope (fig. 7) whereas soil conductivity, soil nitrate, and soil organic matter concentration decreased up the slope (fig. 8). The soils texture, P, and Mg, varied little in relation to the slope. Three types of tissue (new growth, year-old growth, and several-years-old growth) were collected, ground, and the rubber and resin were extracted using the methods of

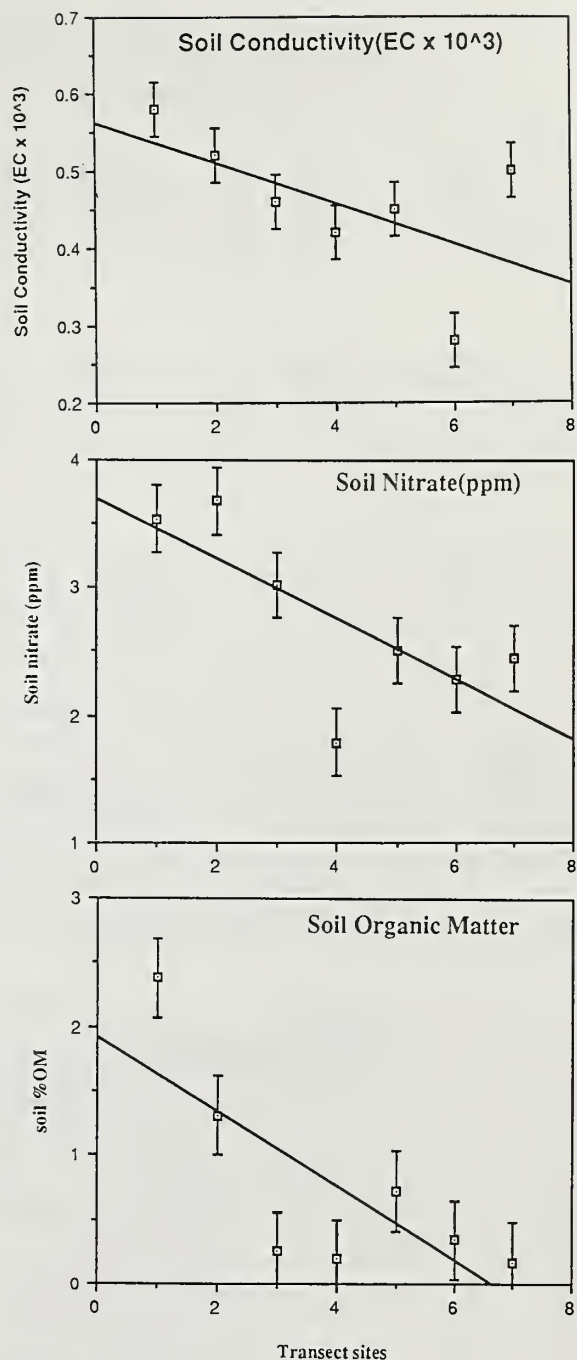


Figure 8--The conductivity ($\text{EC} \times 10^3$), nitrate and organic matter in the soil from seven sites along a water stress gradient in Kingston Canyon south of Richfield, Utah. The lines were drawn by the method of least squares. Vertical lines represent standard error bars.

Table 1--Correlation table (r squared) for rubber and soil factors for three different age tissues of Chrysothamnus nauseosus ssp. hololeucus in relations to the stress gradient

Rubber

Age of tissue	% OM	pH	EC x 10 ³	Na	P	Nitrate	K	Ca	Mg	Clay	Silt	Sand
Green tissue	0.01	0.05	0.31	0.12	0.24	0.02	0.22	0.01	0.08	0.18	0.10	0.03
Year old tissue	0.24	0.04	0.03	0.22	0.02	0.44*	0.02	0.05	0.47*	0.01	0.01	0.03
Old tissue	0.03	0.16	0.01	0.18	0.26	0.14	0.24	0.21	0.36	0.20	0.03	0.13

Resin

Green tissue	0.43*	0.05	0.55	0.05	0.11	0.26	0.02	0.45*	0.03	0.13	0.01	0.02
Year old tissue	0.18	0.17	0.21	0.11	0.36	0.02	0.07	0.03	0.22	0.03	0.01	0.01
Old tissue	0.14	0.16	0.19	0.14	0.55	0.004	0.02	0.18	0.14	0.03	0.18	0.12

* p < .05

Hegerhorst and others (1987c). The Ph of the soil at the different collection sites was 7.9 ± 0.03 (SE). Correlation analyses (r^2 values) of the different elements and properties of the soil with the rubber and resin content are listed in table 1 (Statview 512 1986). In the case of rubber in the year-old tissue, nitrate and Mg had a significant correlation ($p < 0.05$) (table 1). In the green tissues, significant correlation ($p < 0.05$) occurred between resin content and organic matter and Ca. However there were inconsistencies between the different tissues and the interpretation of the data is difficult.

RUBBER AND RESIN CONTENT AFTER TREATMENT WITH BIOREGULATORS, HIGH SALT, AND WATER STRESS

A controlled temperature chamber was used to grow transplanted seedlings of C. nauseosus ssp. consimilis. The 8-month-old plants (ten replicates) were treated with the following bioregulators: paclobutrazol (Pac) (2RS, 3RS)-1-(4-chlorophenyl)-4-4-dimethyl-2-1,4-triazol-yl-pentan-3-ol, XE-1019 [(E)-1-(4-chlorophenyl)-4-4-dimethyl-2-1,1-triazol-yl-penten-3-ol] Flurprimidol (Fl), [alpha-(1-methylethyl)-alpha-[4-(trifluoromethoxy) phenyl]-5-pyrimidine-methanol], 2-(3,4-dichlorophenoxy)-triethylamine (DCPTA), to determine their effect on rubber and resin content. The bioregulators except DCPTA were applied as a soil drench at a dose of 150 µg per pot. DCPTA was applied as a spray (5,000 ppm) to the foliage. Also, plants (ten replicates) were treated with 0.5 M NaCl and with water deficiencies (50% normal water) to cause stress. Results (fig.9) indicated that there was a significant ($p < 0.05$) increase in resin content in plants or the initial plants. In the case of rubber (fig. 9), there was a significant ($p < 0.05$) decrease in the rubber content of the Pac-treated plants. Yokoyama and others (1986) reported an increase in rubber content in guayule plants treated with 2-(3,4-dichlorophenoxy)-triethylamine (DCPTA). Yokoyama and others (1986) used 100 ppm DCPTA on seeds and 2,000 ppm on 18-month-old guayule plants. We used 5,000 ppm of DCPTA and did not obtain a response in rubber rabbitbrush. Further studies using different dosages, application methods, and timing of

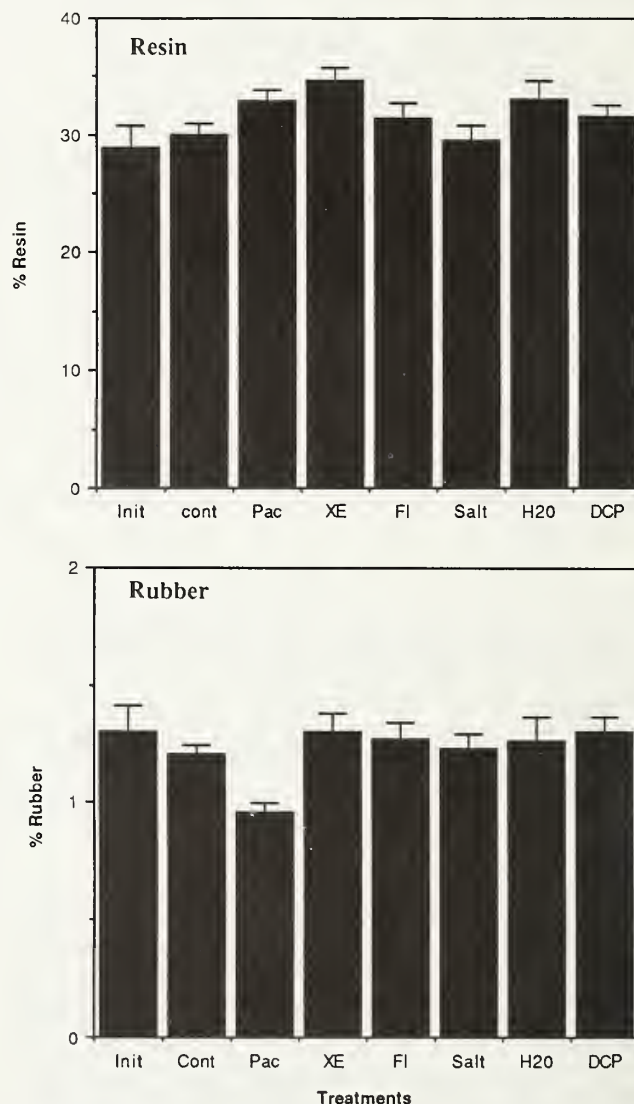


Figure 9--Resin content (upper) and rubber content (lower) of Chrysothamnus nauseosus ssp. turbinatus treated with different bioregulators and stress factors: Cont = untreated control; Pac = paclobutrazol (150 mg); XE = XE-1019 (150 mg); Fl = flurprimidol (150 mg); Salt = 0.5 M NaCl; H₂O = water stress treatments; DCP = DCPTA as a 5,000 ppm foliar spray.

bioregulator treatments are needed to fully assess the possibility of chemically regulating rubber content in rubber rabbitbrush. The rubber content did not increase under the level of water stress that we caused in our plants. Further studies at different levels of water stress are needed.

METABOLIC PATHWAYS OF RUBBER AND RESIN SYNTHESIS

The pathway of rubber synthesis has been associated with the mevalonic acid pathway. The pathway (fig. 10) involves branching around *cis*-isopentenyl pyrophosphate to either rubber or monoterpenoids (Robinson 1980).

Benedict and others (1986) found that the enzymatic synthesis of rubber in guayule was cold induced and that the enzymatic incorporation of isopentenyl pyrophosphate occurs on the surface of rubber particles. The rubber synthesis did not begin until the cool months of October and November. The enzymatic activity of *cis*-isopolyisopolymerase was related to the number of hours of 10°C and below. While the process of rubber synthesis in rubber rabbitbrush has not been studied as extensively as in guayule, it is obvious that regulator genes for the *cis*-isopolymerase in rubber rabbitbrush would have to function in response to heat or stress signals rather than cool temperatures. Although not clearly demonstrated, evidence suggests that the pathway from mevalonic acid to *cis*-isoprene is more closely tied with the formation of some terpenes than that of others. The significance

of elucidating the exact relationship that exists between the resin and rubber formation is the potential of changing the flow of metabolites from monoterpenoids into natural rubber. If environmental signals such as high temperature, low moisture levels, and water stress could be imitated, it may be possible to favor the conversion from mevalonic acid to *iso*-pentenyl pyrophosphate and certain triterpenoids to natural rubber, rather than to monoterpenoids.

CONCLUSIONS

Rubber and resin contents of rubber rabbitbrush vary considerably depending upon tissue type, time of year, and growing conditions. Enhanced rubber production may be a stress response, which suggests the possibility of imposing stress treatments to increase rubber content. The possibility of using bioregulators to chemically alter rubber and resin contents of rubber rabbitbrush also exists. Whether any of these treatments would be commercially feasible remains to be determined.

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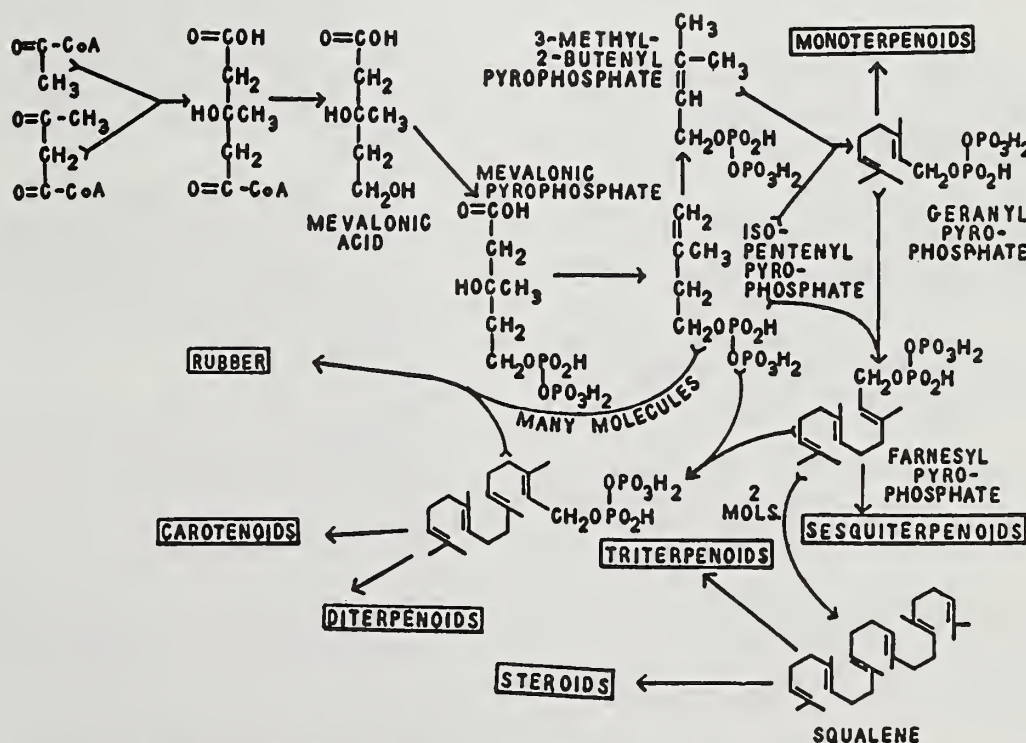


Figure 10--Simple diagram of pathways to resin and rubber compounds. Modified from Robinson 1980.

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